POPULATION ECOLOGY OF NORTHERN BOBWHITES

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Travis Hayes Folk

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DISSERTATION ABSTRACT

POPULATION ECOLOGY OF NORTHERN BOBWHITES

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The longleaf pine (*Pinus palustris*) ecosystem is an ecologically significant region of North America, yet its geographic extent has been greatly reduced by several factors including anthropogenic fire suppression. There is, however, increasing interest in restoring longleaf pine forests, and this necessarily entails the use of prescribed fire. Longleaf pine forests naturally burned as a result of lightning-ignited fires in late spring and early summer (referred to as growing season burns), yet land managers in the Southeast have historically used prescribed fire in late winter (referred to as dormant season fire) to avoid detrimental effects of growing season fire on wildlife, especially nesting game birds like northern bobwhite (*Colinus virginianus*). While research is indicating season of burn can have substantial effects on the plant community of longleaf pine forests, less is known about the influence of season of burn on the life history of native and endemic vertebrates in the longleaf pine ecosystem. Because federal and state agencies are charged with management of public lands, which may entail management for the native ecosystem and game species, it is important to establish the influence of season of burn on animal species. Thus, we undertook a study at Conecuh National Forest (CNF), Alabama to evaluate productivity, survival, and population dynamics of northern bobwhites in longleaf pine forests burned during the growing and dormant seasons.

Aspects of Northern Bobwhite productivity at CNF were similar and dissimilar to other studies conducted elsewhere in their geographic range. Nest success at CNF did not vary appreciably with time since most recent prescribed fire or season of last prescribed fire, but nests in areas that had burned, regardless of season of burn, were 1.8 times more likely to survive a day-length interval as were nests in unburned longleaf pine forests. Estimated nest success was 47.0% over a 23-day incubation period, one of the highest estimates in the published literature. Of Northern Bobwhites that survived through the nesting season (1 September), 17.9% of males and 27.3% of females had hatched ≥ 1 nest. Published estimates of reproductive success for males are similar to those documented at CNF, yet most other published estimates for females are ≈ 75%. Future work should investigate causes for low female reproductive success.

Daily survival rate of Northern Bobwhites was explained by several factors: daily mobility, season of burn, and timber type. Extent of daily mobility had the greatest influence on survival of Northern Bobwhites at CNF, and daily survival decreased as daily mobility increased. Northern Bobwhites in growing season burned longleaf pine forests were 1.5 times more likely to survive each day than individuals in dormant season burned longleaf pine forests. Of several timber types (pine, pine-hardwood, upland hardwood, bottomland hardwood, and miscellaneous areas [food plots, etc.]), Northern Bobwhite daily survival was highest in pine stands. Daily movement rate varied by season of year and whether an individual was associated with an area of unburned habitat. Daily mobility of Northern Bobwhites varied intra-annually, and was greatest in late spring prior to the breeding season. Northern Bobwhites associated with food plots were less mobile than those not associated with food plots.

Based on a literature review and demographic analyses described above, we constructed several matrix population models for Northern Bobwhites. Population models based on a literature search indicated that observed variation in productivity can have the greatest observed impact on population growth rate, yet changes to survival rates in the non-breeding season has the greatest potential impact on population growth rate. Population models based on demographic rates estimated for the CNF Northern Bobwhite population suggest a similar dynamic: increases in non-breeding season survival has the largest potential influence on population growth rate.

In summary, Northern Bobwhite survival is highest in longleaf pine forests burned during the growing season at an approximate triennial frequency, and placement of unburned vegetation within this landscape will also increase survival via reduced mobility on Northern Bobwhites. General research on Northern Bobwhite population management has typically focused on maintenance of suitable nesting and brood rearing habitat, yet population models for the CNF Northern Bobwhite population suggests that increases in survival between breeding seasons can also be important for increasing population growth rate.

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Style manual or journal used *Encyclopedia of Southern Fire Science*, *Journal of Field Ornithology*, *The Auk*, *The Condor*, *Population Ecology*, *Ecology*

Computer software used ArcCatalog 8.3, ArcMap 8.3, ARC/VIEW 3.2A, DNRGarmin 5.1.1, Locate II, Maple 9.5, MathType 5.2, Microsoft Excel 2002, Microsoft Word 2002, Poptools 2.6, SAS 9.1, SigmaPlot 8.0

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I. REVIEW OF FIRE EFFECTS ON NORTHERN BOBWHITES (*Colinus virginianus*)

INTRODUCTION

Northern bobwhites are a popular and economically important game species throughout much of their range (Burger et al. 1999) and they inhabit a variety of habitat types throughout most of the eastern United States and northeastern Mexico (Brennan 1999). Preferred vegetation types range from landscapes dominated by agricultural activities (Roseberry and Klimstra 1984), arid regions of western Texas and Oklahoma (Lehman 1984), and southern pine forests (Stoddard 1931, Rosene 1969). This wide assortment of plant assemblages share a common habitat structure of a sparse to open overstory canopy coupled with an expansive herbaceous and shrubby ground cover. In many of these habitats, especially forested areas, fire is an integral part of maintaining plant structure and composition suitable to northern bobwhites (Stoddard 1931, Speake 1967, Rosene 1969, Burger 2001). In the 1920's, Herbert Stoddard began the first research on the effects of prescribed fire on aspects of the bobwhite's life history and habitat. This work was conducted in pine forests of southern Georgia and northern Florida and demonstrated the benefits of fire to bobwhite populations. This initial research was summarized in the book *The Bobwhite Quail: its habits, preservation, and* *increase* (Stoddard 1931). Despite recognition of the beneficial influence fire has on bobwhite habitat and populations in general, details of the specific demographic pathways that fire maintained habitats influence bobwhite life history are less well known.

While the timing of natural fire likely varied throughout the bobwhite's range, the longleaf pine (*Pinus palustris*) ecosystem (Frost 1993) was maintained by natural lightning-ignited fires in the late spring and early summer months of May and June (Komarek 1964). Recent research indicates that timing of fire during the year, whether in the traditional period for prescribed fires in February and March or during the natural timing of fires in May to June, can have a profound impact on habitat structure, plant species presence and abundance, and can influence timing of critical life history events in plant species, such as flowering (Robbins and Myers 1992). Prior to European settlement, bobwhite habitat in the Southeastern Coastal Plain was primarily dominated by the longleaf pine ecosystem (Wahlenberg 1946, Frost 1993). Longleaf pine habitats were characterized by an understory of mostly grasses, especially wiregrass (*Aristida* spp.) and broomsedge (*Andropogon virginianus*), and legume species plus scattered shrubby species. The midstory was absent or minimal, and the overstory was predominantly longleaf pine, with slash pine (*Pinus elliottii*) occasionally on wetter sites (Peet and Allard 1993). These areas were characterized as "park-like" by early explorers and this habitat structure was maintained by frequent fire during late spring and early summer (McPherson 1997, Komarek 1964, Glitzenstein et al. 1995, Frost 1998). Natural fire during this time of year was likely caused by increased lightning activity (Komarek 1964).

FIRE AND BOBWHITE SURVIVAL

Bobwhite mortality due to consumption by fire is rare, especially for healthy individuals (Carter et al. 2002). Bobwhite chicks begin to fly by 2 weeks of age (Brennan 1999); therefore, bobwhites are susceptible to fire related mortality for only a small portion of the life cycle. Field observations suggest that bobwhites will move in advance of a fire and occasionally escape by flight into surrounding wetlands less likely to be consumed by fire (*T. H. Folk, personal observation*).

Relatively few studies have evaluated the impacts of post-fire vegetative recovery on survival of bobwhites. Although several reports suggest that potential predators of bobwhites may be attracted to areas immediately post-fire (Tewes 1984, Mueller and Atkinson 1985), there is little evidence that this influences mortality of bobwhites. Mueller et al. (1988) investigated differences in survival rates of bobwhites in the Coastal Plain of Georgia in mature longleaf pine forest with small agricultural fields interspersed throughout the landscape. They evaluated survival of bobwhites for 30 days prior to and 30 days following prescribed fire in two treatment areas. Treatments consisted of one area that was burned completely (469 acres) and a second adjacent area that received an incomplete burn (i.e., patchy burn treatment, 247 acres) by protecting patches of vegetation from fire. These patches ranged in size from 0.5-2.0 acres, and are commonly recommended to provide protective post-fire cover for bobwhites (Rosene 1969, Landers and Mueller 1986). Both areas were burned during mid-March in 1985 and 1986. Survival of bobwhites 30-days post-fire did not significantly decrease in areas with patchy burns as compared to clean burned areas. Despite the lack of difference in survivorship, the authors suggest that areas protected from fire are still advisable as a component of a land management plan for bobwhites since patches provide "other contributions to habitat quality of bobwhites (Mueller et al. 1988:254).

Other studies concerning the influence of prescribed fire on bobwhite survival have been conducted in Texas, yet none have documented differences in bobwhite mortality when pre- and immediate post-burn results are compared. Carter et al. (2002) reports on bobwhite survival in the Edwards Plateau region of central Texas. Radio-marked bobwhites were monitored for 6 months post-fire in treatment areas (i.e., burned pastures, 148-702 acres) and control areas (i.e., pasture left unburned) that surrounded the treatment areas. Bobwhite survival was similar between burned and unburned pastures. Hernández et al. (2003) report similar results for bobwhites in the ecotonal area of the Rolling Plains and Cross Timbers ecoregions in Texas. Control of prickly pear cactus (*Opuntia* spp.) is of management concern in this region, and control techniques typically involve prescribed fire, followed immediately by herbicide application. They compared bobwhite survival for 2-3 years in areas burned and treated with herbicides (1110 and 1203 acres) to control areas (1337 and 1962 acres) that received neither management action. Bobwhite survival did not differ between the treatment and control areas.

FIRE AND APPARENT ABUNDANCE OF BOBWHITES

Initial inference as to the positive impact prescribed fire has on bobwhite populations came from repeated observation and trapping of birds (e.g., Stoddard 1931, Speake 1967). While these studies did not control for potential biases in detectability of bobwhites (Williams et al. 2001), they provide useful insights about the effect prescribed fire has on bobwhite populations.

Stoddard (1931) was arguably one of the first biologists to recognize and promote the beneficial nature of prescribed fire to bobwhite populations. While Stoddard recognized the valuable nature of fire to bobwhites, he also acknowledged the complexity of the relationship (Stoddard 1931:402). Pursuant to this charge, Speake (1967) and others conducted lengthy investigations into the use of dormant season prescribed fire (February and March) in the Piedmont region of the Southeast. Speake (1966, 1967) reported on a 16-year study on abandoned agricultural lands in the Piedmont of Alabama where approximately half of the area (124 acres) was burned on 1-4 year rotations between 1950 and 1966. Over the same time period, fire was withheld from the control area (133 acres), which was of a similar agricultural history. At the end of the study, Speake (1966) estimated that bobwhites on the treatment area had increased over the study period while on the control area birds were rare. Findings similar to those of Speake (1966, 1967) have been reported for bobwhites in the Interior Low Plateau in Kentucky (Scott 1959), the Central Tallgrass Prairie in Iowa (Seitz and Landers 1972), and the Rolling Plains in Texas (Renwald et al. 1978, Leif and Smith 1993). Engstrom et al. (1984) reported that bobwhites were rare or not present in the breeding season nine years after fire had been excluded from a mature old-field mixed pine forest in the Coastal Plain of Florida.

For the past seven to eight decades, fire was primarily applied for bobwhite management during the late winter months of February and March, the end of the dormant season (Stoddard 1931, Rosene 1969). Prescribed fire is still used more frequently during late winter than during the growing season, when naturally occurring fires were more likely (Brennan 1994, Johnson and Hale 2000). This was motivated by the belief that growing season burns might 1) destroy nests that are potentially on the ground in spring and summer months (Stoddard 1931, Rosene 1969), 2) eliminate residual seeds from late winter when other bobwhite food sources might be scarce (Rosene 1969), 3) extend the amount of time that protective cover was not available for bobwhites (Robbins and Myers 1992), and 4) completely kill vegetation, particularly legumes, that had begun to grow (Rosene 1969). Recent findings suggest that growing season fires may actually benefit bobwhites (Engstrom et al. 1996, Brennan et al. 2000), despite long held dogma (Stoddard 1931, Rosene 1969).

Brennan et al. (2000) evaluated the initial effects of growing and dormant season prescribed fire on bobwhites on well-managed quail plantations in the Coastal Plain of Georgia and Florida. Preliminary results indicated that hunting success was slightly greater on areas burned in May than in areas burned during February and March, although similar patterns were not obvious by the third year post fire (Brennan et al. 2000). In addition, Engstrom et al. (1996), reported on the difference of dormant and growing season fire on bobwhites in longleaf pine forests in the Coastal Plain of Florida and North Carolina. Initial results indicated that bobwhites occurred in areas burned during the dormant season, but were not detected in areas burned during the growing season. However, forest structure in growing season burns had attributes closer to that of quality bobwhite habitat (i.e., abundant herbaceous and shrubby understory and minimal midstory), and other species common to well managed longleaf pine forests (e.g., Bachman's sparrow, *Aimophila aestivalis*) were not negatively influenced by growing season fire. Rosene (1969), however, suggested that severe spring fires on properties in the Lower Coastal Plain of South Carolina and the Upper Coastal Plain in Alabama led to reductions in bobwhite coveys the following fall.

Interest has increased recently in the re-introduction of fire as a component of restoration of pine-grassland habitats in the Southeast. Although attention to restoration has primarily been driven by habitat requirements for the red-cockaded woodpecker (*Picoides borealis*), a federally endangered species, several studies suggest that bobwhites respond positively to habitat management for red-cockaded woodpeckers which entails development of an abundant herbaceous and shrubby understory and reduced midstory in pine dominated forests (Brennan et al. 1995, Engstrom and Baker 1995, Wilson et al. 1995).

In other studies, Provencher et al. (2002) evaluated bobwhite response to three treatments to reduce hardwood midstory in longleaf forests in northwest Florida: growing season fire, herbicide application followed by dormant season prescribed fire, and felling-girdling of hardwoods followed by dormant season prescribed fire. They examined the avian community in the third and fourth years after treatment. Bobwhites were detected more frequently on treatment plots than control, although none of the three restoration techniques appeared to be significantly more effective (Provencher et al. 2002). Cram et al. (2002) reports similar findings from restoration of shortleaf pine (*Pinus echinata*) forests in the Ouachita Mountains, Arkansas. These stands had previously been unmanaged, and the treatments included: control stands, mechanically thinned stands with no fire, thinned and burned stands 1 year post fire, thinned and burned stands 2 years post fire, and thinned and burned stands 3 years post fire. Treatment stands were burned during the dormant season. Surveys suggested that bobwhite abundance was greater in burned stands than thinned stands without fire, and bobwhites were most numerous in stands during the third growing season after a burn. All treated stands contained more bobwhites than did control stands (Cram et al. 2002).

FIRE AND BOBWHITE NESTING BIOLOGY

In the southeastern US, growing-season fire coincides with timing of reproduction for bobwhites (May through August; Stoddard 1931, Speake 1967), making egg mortality highly likely in burned areas. This initially motivated land managers in the Southeast to burn during the late winter months of February and March (Stoddard 1931, Rosene 1969). However, bobwhites can lay multiple nests in a single breeding season (Stanford 1972, Curtis et al. 1993, Burger et al. 1995), so if a nest is destroyed by fire the female will likely re-nest. The probability of re-nesting, however, declines as the breeding season advances. Females that have a nest destroyed in a late summer fire are less likely to re-nest. The population level effect of fire induced nest loss is not well studied. It is obvious that natural populations can persist with a natural fire frequency of 2-8 years (Stoddard 1931, Frost 1998); however, the effects of repeated, shorter rotations of growing season fire are unknown. The influence of nest loss due to fire likely depends on size of burned area, season of burn, fire intensity, and length of fire rotation. In addition, conditions following a burn, such as drought and extreme rain events, may interact with and alter the significance of season of fire to bobwhites. These factors have received little research attention.

Despite the importance of nesting and brood habitat to sustainable bobwhite populations (Dimmick et al. 2002), relatively little work has evaluated how prescribed fire influences a variety of aspects of bobwhite nesting ecology. Investigations have focused on nesting occurrence, nest survival, and quality of brood habitat. Dimmick (1972) in the Coastal Plain of Tennessee and Simpson (1972) in the Coastal Plain of Georgia reported that nests were less frequent in areas that had not experienced at least one growing season since burning. Bobwhites nests are often in close association with bunch grasses (e.g., wiregrass, broomsedge) and are normally woven from plant material, typically dead grass leaves, to create a dome that surrounds the incubating bird (Stoddard 1931, Klimstra and Roseberry 1975). Dimmick (1972) and Simpson (1972) suggested that a lack of dead vegetative material in burned areas that had not experienced at least one growing season resulted in fewer bobwhite nests in these areas as compared to burned areas that had experienced ≥ 1 growing season since burn. This observed pattern could have been due to movement out of burned areas or decreased nesting effort.

Although some bobwhite nests are consumed during prescribed fire, several studies have evaluated nesting success in post-fire vegetative conditions. Carter et al. (2002) reports on nesting success in the Edwards Plateau region of central Texas in areas that were either burned (148 to 702 acres) or unburned (areas surrounding burned treatments). Areas were burned in January or February, and nest success was monitored in the following breeding season. Carter et al. (2002) reported no significant differences in nest success between burned and unburned areas. Hernández et al. (2003) came to similar conclusions for bobwhites in the Rolling Plains and Cross Timbers regions of western Texas. Dimmick (1972) also found no difference in nest success between burned and unburned areas in old-field habitats of Tennessee. While some of the studies mentioned had small sample sizes, all are consistent in failing to demonstrate a reduction in nest success due to an attribute of prescribed fire.

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II. ASPECTS OF PRODUCTIVITY OF NORTHERN BOBWHITES IN LONGLEAF PINE DOMINATED LANDSCAPES

ABSTRACT. Longleaf pine forests once provided habitat for Northern Bobwhites in the Southeastern Coastal Plain of the US, but both Bobwhite populations and the extent of quality longleaf forest has been greatly reduced. I studied aspects of Northern Bobwhite productivity in a landscape dominated by longleaf pine forests which were managed with triennial prescribed fire for habitat management purposes. I investigated how habitat-related covariates, such as whether the stand was managed with growing or dormant season prescribed fire, or individual covariates, such as sex and age of the incubator and nest initiation date, explained patterns in daily nest survival. Estimated nest survival was 0.47 (95% CI, 0.34 to 0.64) for a 24-day incubation period; however, neither habitat nor individual related covariates explained substantial variation in daily nest survival. Of radiomarked females that survived the breeding season, 27.3% hatched ≥ 1 nest. Compared to similar studies elsewhere in the geographic range of Bobwhites, nest survival in our study was high, although the proportion of females successfully incubating and hatching ≥ 1 nest in a season, given that they survived the breeding season, was lower than that estimated for other Bobwhite populations. Future work should investigate whether the corresponding high nest survival and low female

nesting success is sufficient to allow for population persistence in fire-maintained longleaf pine habitats.

INTRODUCTION

Northern Bobwhites (*Colinus virginianus*; hereafter Bobwhite[s]) are a well-studied gallinaceous bird that inhabits early successional habitats throughout the eastern US and northeastern Mexico (Brennan 1999). Declines in Bobwhite populations have however been occurring range wide for at least the last four decades (Sauer et al. 2004) with the cause widely believed to be habitat conversion or degradation away from early successional habitats (Hunter et al. 2001). In the Southeast, the longleaf pine ecosystem once constituted a substantial portion of the Bobwhite's range (Frost 1993), and provided quality early successional habitat to Bobwhite populations. Similar to Bobwhites however, the longleaf pine ecosystem has declined significantly from its pre-Columbian extent of approximately 37 million ha to only 3-5% of its former range (Frost 1993). There is increased interest in restoring both Bobwhite populations (Dimmick et al. 2002) and longleaf pine forests (Kirkman et al. 2004) throughout their respective geographic ranges. Restoration and management of longleaf forests therefore also will increase the likelihood of restoring populations of Bobwhites and other declining endemic species of the longleaf ecosystem (Tucker et al. 2003).

Efforts to conserve avian species require accurate demographic estimates. Further, conservation and management efforts can be more effective when an understanding is gained of how demographic attributes may vary with different management scenarios. Management of longleaf pine forests centers principally around frequent use of prescribed fire (i.e., every 1-4 years; Robbins and Myers 1992). Use of prescribed fire also can vary from the traditional timing of late winter (i.e., February and March; Johnson and Hale 2002) to the more natural period of late spring and early summer (Komarek 1964, Robbins and Myers 1992). Biologists interested in game species have preferred using prescribed fire during late winter partly because it avoids destroying ground nests of many bird species, especially Bobwhites and Eastern Wild Turkeys (*Meleagris gallopavo*), while biologists interested in endangered species (e.g., red-cockaded woodpeckers [*Picoides borealis*]) are increasingly using prescribed fire in late spring and summer because it mimics natural conditions of the longleaf pine ecosystem (Komarek 1964). Given Bobwhites can be exposed to a variety of post-fire conditions (i.e., 1 day to several years post burn of either a dormant or growing season fire), it is important to explore and quantify attributes of their demography with respect to use of prescribed fire in order to better guide management efforts.

Our objective was to estimate different demographic attributes that contribute to productivity of Bobwhite populations in a landscape dominated by longleaf pine forests and managed with prescribed fire. First, I describe Bobwhite nesting ecology in this habitat type. Second, I estimate nest survival and explore the potential relationship of prescribed fires to that estimate. Finally, I place attributes of Bobwhite nesting ecology estimated in this study into the context of similar estimates for Bobwhites throughout their geographic range.

METHODS

Study area. I studied Northern Bobwhites at Conecuh National Forest (CNF) in Covington and Escambia counties, Alabama (31.1°N, 86.6°W). CNF is located in the Southeastern Coastal Plain physiographic region and covers nearly 340 km^2, of which approximately 110 km^2 is mature longleaf and mixed longleaf pine-hardwood. Longleaf pine stands in CNF are classified as Pine Hill, Dougherty Plain, or Wet Pine Flatwoods landtype associations (Carter et al. 1999). Because longleaf pine forests in this area have historically not been converted to agricultural uses (Croker 1987), the understory contains shrubby and herbaceous vegetation typical of longleaf forests (Carter et al. 1999). CNF is managed by the US Forest Service with triennial prescribed fire during the growing (mid-March to early September) and dormant (mid-September to early March; Robbins and Myers 1992) seasons. Private holdings within CNF are primarily longleaf and mixed pine-hardwood forests, and they are rarely burned (T. H. Folk, personal observation).

Field methodology. I trapped Bobwhites with welded wire funnel traps in February, March, May, and October from February 2002 to May 2004. Trapped individuals were sexed, aged, marked with a uniquely numbered leg band (size 7, National Band and Tag Co., Newport, Kentucky, USA), and equipped with a necklace-style radio transmitter (model A3900, Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA). Transmitters weighed approximately 6.3 g, had a life expectancy of 300 days, and were equipped with a 4-h mortality switch. Necklace-style transmitters do not impact body mass dynamics or physiology of captive birds (Corteville 1998, Hernández et al. 2004), nor do they decrease survival rates of birds in the wild (Mueller et al. 1988, Corteville 1998, Palmer and Wellendorf in revision, Terhune et al. in revision).

Radio-marked individuals were located ≥ 5 times week^{-1} during the breeding season (i.e., May to September). Bearings for triangulations were typically taken < 150 m from the radio-marked individual. An individual was suspected of incubating a nest when it was repeatedly found in a localized area for 2-3 days. Once nesting activity was suspected, triangulations were taken from a closer distance (30-50 m). After 4-5 days of suspected nesting activity, I attempted to locate the nest during afternoon incubation recesses to avoid disturbing the incubator on the nest. Once the nest was found, clutch size was determined and stage of incubation was estimated by candling eggs (Hanson 1954). Nest sites were marked at some predetermined direction (>10 m) away from the nest. Individuals suspected of or known to be nesting were visited daily to determine, via telemetry, if the incubator was present at the nest. If the incubator was not located at the nest site for 2 consecutive days, the nest was again inspected to determine nest status. Nest status was classified as hatched, depredated, or abandoned. For the purpose of estimating daily nest survival, depredated and abandoned nests were considered to have had the same fate of nest failure.

Statistical analyses. Daily survival rate (DSR) of nests was estimated with the Mayfield estimator (Mayfield 1961) using a maximum likelihood approach (Johnson 1979). Because nests were monitored nearly daily, if a nest was found to have hatched or failed on day *t* (i.e., after 2 days of incubator absence) I assigned survival through day *t*-2 for hatched nests and survival through day *t*-3 and failure on day *t*-2 for failed nests.

Because values reported for nest fate at each observation were binary, I used a binomial distribution of errors and a logit-link function to model survival. I evaluated model adequacy from the global model (i.e., a model that contains all effects included in *a priori* models) with the test described by Hosmer and Lemeshow (1980).

Use of continuous covariates in the logit link assumes a linear relationship between the covariate and the response variable (Hosmer and Lemeshow 2000). Hosmer and Lemeshow (2000: 99) suggest the use of *group-smoothed plots* to evaluate this assumption of linearity. In this procedure, I ranked the observed values for a particular continuous covariate by magnitude and categorized observations by deciles. I then created a 10-level categorical variable to describe classification of the continuous covariate into deciles. The continuous covariate was replaced with its categorical representation in a model. Maximum likelihood estimates of model parameters were then recalculated. A group-smoothed plot is then developed from the resulting beta values for the categorical variable and midpoints of each decile. If the assumption of linearity in a continuous covariate is appropriate the plotted points should be nearly linear. If the plotted points are not linear, the parametric form of the continuous covariate (e.g., quadratic, sigmoid, etc.) will be discernable from the plot, and then transformed appropriately.

I used an information theoretic approach to select among models of nest DSR (Burnham and Anderson 2002). I used Akaike's Information Criterion (AIC) to rank models (Akaike 1973). I did not use Sugiura's (1978) Second-Order form of AIC (AIC_c; frequently referred to as *small sample AIC*; Burnham and Anderson [2002]) because the ratio of sample size to maximum number of estimated parameters was > 40 ($n/K = 68$; Burnham and Anderson 2002). Model comparisons were made with ΔAIC, which is the difference between the lowest AIC value and AIC from all other models (Burnham and Anderson 2002). Models with ΔAIC ≤ 2 have substantial support from the data (Burnham and Anderson 2002). I also computed Akaike weights for each model. Model weights represent the evidence for a particular model being the best model assuming that the best model is among the candidate set (Burnham and Anderson 2002).

I derive inference in two ways from models of nest DSR. First, I compute DSR (and their associated 95% CI) for comparison with other estimates of DSR in the literature. Second, I compute odds ratios for parameters appearing in the best model(s). Odds ratios quantify the likelihood for survival of a nest over a single day in a *comparison state* (e.g., subadults) to nests in the *reference state* (e.g., adults). Odds ratios (and their associated 95% CI) were computed according to Hosmer and Lemeshow (2000).

Covariate and model development. I selected covariates for inclusion into models of daily nest survival based on review of the literature and novel hypotheses regarding the influence of prescribed fire on nesting biology. Most research of Bobwhite nest survival has focused on covariates that describe the micro-site conditions at the nest, although these largely fail to explain substantial amounts of variation in nest survival (e.g., Taylor et al. 1999b, Townsend et al. 2001). Our habitat covariates instead described the stand at a larger scale, and I wanted to evaluate whether heterogeneity in DSR was related to factors at this scale, because land managers are more apt to manage for stand-level conditions rather than micro-site conditions. Habitat related covariates included the following: 1) whether a stand had been managed with prescribed fire or not (BURN), 2) whether longleaf pine stand containing the nest was managed with growing or dormant season prescribed fire or was unburned (BURNSEASON), and 3) number of days elapsed between most recent burn and calendar date of nest initiation (TSB). Prescribed fire is applied triennially in longleaf pine stands at CNF (whether growing or dormant season prescribed fire) whereas nearly all private property was not burned regularly. The majority of private property within CNF had not been burned for at least the previous 10 years (T. H. Folk, personal observation). For nests located in unburned areas, the time since burn (TSB) was calculated from 1 January 1990.

For the purpose of analysis, the initiation date of a nest was calculated relative to the day prior to the day the first nest of the season was detected. This reflects intra-annual differences in breeding season chronology and controls for inter-annual differences in nest initiation. Age and sex of the incubator was also used as covariates in the analysis. Thus, nest and incubator covariates are as follows: 1) relative initiation date of the nest (INIT), 2) age of the radio-marked incubator (AGE), and 3) sex of the radio-marked incubator (SEX). I also included year of the nest (i.e., 2002, 2003, 2004) as a covariate (YEAR). All means are reported with corresponding SE or 95% CI values. I define nest survival as the probability that a nest will survive a 23-day incubation period and hatch. I define nesting success as the proportion of individuals (male and female) that survive to the end of the breeding season (1 September) and hatch ≥ 1 nest in that season.

RESULTS

Collectively, on 1 May I had 92 radio-marked females (23 in 2002, 34 in 2003, 35 in 2004), of which 64% were juveniles and 36% were adults. I monitored 44 nests (22 in 2002, 8 in 2003, 14 in 2004) over 749 exposure days across 549 exposure intervals. First nests of each year were 16 May 2002, 28 May 2003, and 23 May 2004, and initiation date of nests averaged 18 June (±4 days) across all three years. Intra-annual mean initiation date of nests was similar across years (2002: $\bar{x}$ = 18 June, 95CI = 9 June-28 June; 2003: $\bar{x}$ = 25 June, 95CI = 13 June-7 July; 2004: $\bar{x}$ = 22 June, 95CI = 8 June-6 July). There was not a relationship between calendar date of nest initiation of first nests and the linear distance between the nest site and a point central to locations prior to covey breakup (i.e., 15 March to 7 April; $\underline{n}$ = 30, $\underline{r}$ = -0.01). Of nests found in burned areas ($\underline{n}$ = 39), TSB averaged 645 ± 69 days (range: 23 to 2,334 days). Clutch size was similar across years (2002: $\bar{x}$ = 11.75 , 95CI = 10.60-12.90; 2003: $\bar{x}$ = 12.33 , 95CI = 9.79-14.87; 2004: $\bar{x}$ = 11.77 , 95CI = 10.39-13.15), although clutch size did decline with Julian date ($\underline{r}$ = -0.42, n = 20). Mean clutch size across all years of study was 11.75 (±0.61).

Tests of model adequacy suggest the global model adequately describes the data (χ^2 = 6.00, df = 8, P = 0.65). Group smoothed plot for TSB did not suggest a nonlinear form for the relationship between TSB and DSR via the logit (Figure 1). No model performed better than the null model (i.e., a model with no *a priori* effects). Thus, there was not substantial support for any covariate in models of daily survival rate of nests (Table 1). There was some support for a model with AGE and BURN (ΔAIC = 1.498, Table 1). Under the null model, DSR of Bobwhite nests at CNF was 0.968 (SE, ±0.01;

95% CI, 0.96 to 0.98) and nest survival over a 23-day incubation period is 46.9%. BURN was included in the AIC best model set (i.e., ΔAIC < 2). Nests in burned areas were 1.8 (0.6-5.4) times as likely to survive as nests in unburned areas. The effect of burning was positive for nest DSR, but because the confidence interval for the odds ratio encompasses 1.0 the effect was not substantial in our sample.

Of birds that survived until the end of the breeding season (i.e., 1 September; n = 22 and 28 females and males, respectively), 27.3% of females and 17.9% of males had hatched ≥ 1 nest (Table 2). Of the 22 nests that failed, 15 were depredated, 4 were abandoned by the incubator, and for 3 nests the incubator was killed.

DISCUSSION

Nest survival reported in this study (46.9%) is similar to other published estimates elsewhere in the range of Bobwhites. In pine forests of the Southeast, estimates of Bobwhite nest survival for a 23-day incubation period vary from 18% (apparent nest survival; Simpson 1976) to 51.1% (Mayfield estimate; Burger et al. unpublished manuscript). Our estimate of nest survival is also similar to that of Bobwhites on areas with intensive management (45%; DeVos and Mueller 1993). Studies examining habitat attributes that may influence nest survival in Bobwhites have primarily focused on nest micro-site conditions. For example, Townsend et al. (2001) failed to find a consistent relationship between successful and un-successful nests with 18 vegetative variables describing nest micro-site conditions of Bobwhites in Oklahoma. Taylor et al. (1999b) came to similar conclusions for nesting Bobwhites in Kansas. Our analysis approached variation in nest survival from conditions that vary as a result of differences in the timing of the use of prescribed fire. I, however, failed to find support for variables describing variation in use of prescribed fire (i.e., variation observed in this study) or covariates specific to the incubator (Table 1). Similar results have been found elsewhere in the range of Bobwhites. Both Carter et al. (2002) and Hernández et al. (2003) did not detect differences in apparent nest survival between burned and unburned areas in western Texas. Dimmick (1972) also failed to find differences in apparent nest survival between burned and unburned old-field habitats of Tennessee. Carter et al. (2002) and Dimmick (1972) considered burned areas that had received prescribed fire the January-February and March, respectively, prior to the breeding season. Hernández et al. (2003) considered burned areas that had received fire 2 and 3 winters (February 1995) prior to the breeding seasons of interest (1997 and 1998). Using artificial ground nests, Jones et al. (2002) did not find a difference in nest survival between unburned and burned (i.e., burned 4-5 months prior to artificial nest trials) longleaf pine habitat. Given that Bobwhites appear to construct nests in areas with greater ground level concealment (Taylor et al. 1999a), attributes of the surrounding habitat, as influenced by management with prescribed fire, do not appear to substantially influence the probability of a successful nesting attempt. Although, Dimmick (1972) and Simpson (1972) suggested Bobwhites nest less frequently in areas that have not experienced at least one growing season between a fire and the breeding season. The lack of dead herbaceous vegetation in recently burned areas appears to not provide suitable nesting substrates for Bobwhites. Future research should better evaluate the relationship between the spatial extent of fire, Bobwhite nesting effort, and the potential population level influence.

Increasing attention is being given to dispersal processes in gallinaceous species (e.g., Badyaev et al. 1996, Townsend et al. 2003, Keppie 2004, Yoder et al. 2005). One central focus of this attention is the cost and benefit of dispersal. For example, Badyaev et al. (1996) found that Eastern Wild Turkeys that covered larger areas after break up of flocks but prior to the first nesting attempt had higher nest survival, which was likely due to increased habitat sampling. Recent work suggests that, in general, dispersal in Bobwhites is not costly as it does not appear to decrease survival (Townsend et al. 2003, Cook 2004) or influence reproductive success (Townsend et al. 2003). Similar to these findings, I did not find evidence that initiation date of first nests was related to a measure of dispersal (i.e., linear distance between nest location and a point central to a series of locations during the covey period). However, sample size was not large in our analysis. Further, reproductive costs of dispersal (e.g., depleted energy reserves; Danchin and Cam 2002) could be masked due to dispersers suffering greater mortality than non-dispersing individuals (Chapter III).

Species that experience low annual survival are able to persist because of correspondingly high levels of annual fertility (Sæther and Bakke 2000). Northern Bobwhites are aptly described by this type of demographic structure (Chapter III), and their high fertility is due to multiple nesting attempts in a single breeding season (DeVos and Mueller 1993). Burger et al. (1995) suggested that reproductive effort in Bobwhites might normally be great enough such that any female surviving the breeding season will have successfully hatched ≥ 1 nest over the breeding season. Evidence supportive of this claim can be found in several studies in Iowa (Suchy and Munkel 1993), Missouri

(Burger et al. 1995), Oklahoma, (Cox et al. 2005), Georgia (Burger et al. unpublished manuscript), and Florida (DeVos and Mueller 1993). In these studies, approximately 72% of females that survived the breeding season successfully hatched ≥ 1 nest (Table 2). Results of this study and those of Taylor and Burger (1997) report a smaller proportion (25%) of females that survived and hatched ≥ 1 nest in a season. Interestingly though, despite disparity in the proportion of females hatching a nest among studies, the proportion of males that survive a breeding season and hatch ≥ 1 nest appeared similar (Table 2).

Several explanations exist that may account for differences in nesting success of female Bobwhites. First, differing proportions of females may not attempt to nest during a breeding season, although this is unlikely given the life history of Bobwhites. In fact, Bergerud (1988), in a review of North American grouse species, suggested that indeed most females likely do attempt or are capable to breed in a given season. Review of other avian species with demographic attributes similar to Bobwhites suggests that large proportions of females should attempt to breed in a season (Sæther and Bakke 2000). Second, differences in nest survival could contribute to the lower proportion females that survive the breeding season and hatch ≥ 1 nest. However, this is also unlikely to account for most of the difference in nesting success because nest survival estimates across the studies were similar and nest survival estimates were not consistently lower for this study and Taylor and Burger (1997), as compared to other studies (Table 2). Third, decreased nest survival during the egg laying period may account for lower estimates of nesting success in this study and Taylor and Burger (1997). No unbiased estimate of nest survival (i.e., estimates not based on apparent survival) during egg-laying exists for Bobwhites. Fourth, while it is likely that most females attempt to nest in a season, the degree to which multiple nests are laid may explain some of the differences in nesting success in female Bobwhites presented in Table 2. The above factors, collectively or singularly, could contribute to the low female success documented in this study.

Conservation efforts for Bobwhites and other species inhabiting early successional habitats are primarily geared towards development and management of suitable habitat. Results of this study and others conducted elsewhere throughout the range of Bobwhites suggests that timing during the annual cycle and the interval between prescribed fires does not have an influence on nest survival of Bobwhites. I found limited evidence of higher DSR in burned areas as compared to unburned areas. Although this is not a direct index of population productivity, it does suggest that management of longleaf forests with prescribed fire does not negatively influence an important aspect of Bobwhite productivity.

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Table 1. Models of daily nest survival rate for Northern Bobwhites at Conecuh National Forest, Alabama, 2002-2004. The null model contained only an intercept value and can be regarded as a model with no covariates. Delta AIC quantifies the relative support for a given model with models having ΔAIC ≤ 2 having substantial support from the data. Akaike weights evaluate the degree of evidence in support of a model given that one of the models is the best model amongst the candidate set.

Model	*K*	Log($\mathcal{L}$)	AIC	ΔAIC	Akaike weight
Null	1	-94.96	191.925	0	0.190
AGE	2	-94.16	192.331	0.406	0.155
BURN	2	-94.48	192.980	1.056	0.112
TSB	2	-94.55	193.108	1.184	0.105
AGE BURN	3	-93.70	193.423	1.498	0.090
SEX	2	-94.76	193.545	1.620	0.084
INIT	2	-94.94	193.889	1.964	0.071
AGE INIT	3	-94.05	194.122	2.198	0.063
BURNSEASON	3	-94.24	194.511	2.586	0.052
SEX BURN	3	-94.44	194.911	2.987	0.043
SEX INIT	3	-94.68	195.391	3.466	0.034
Global[a]	8	-92.74	201.673	9.748	0.001

[a] Global model included all of the *a priori* effects [i.e., AGE=age(juvenile or adult) of incubator, BURN=whether a stand had managed with prescribed fire or not, TSB= number of days elapsed between most recent burn and initiation date of the nest, SEX=sex of incubator, INIT= relative initiation date of the nest, BURNSEASON= whether the most recent fire in a stand was conducted during the growing or dormant season or the area was unburned (the unburned condition was included in the coding for BURNSEASON).

Table 2. Comparisons of nesting success of Northern Bobwhites populations throughout their geographic range. Estimates of nesting success are derived from radio-marked samples of Bobwhites.

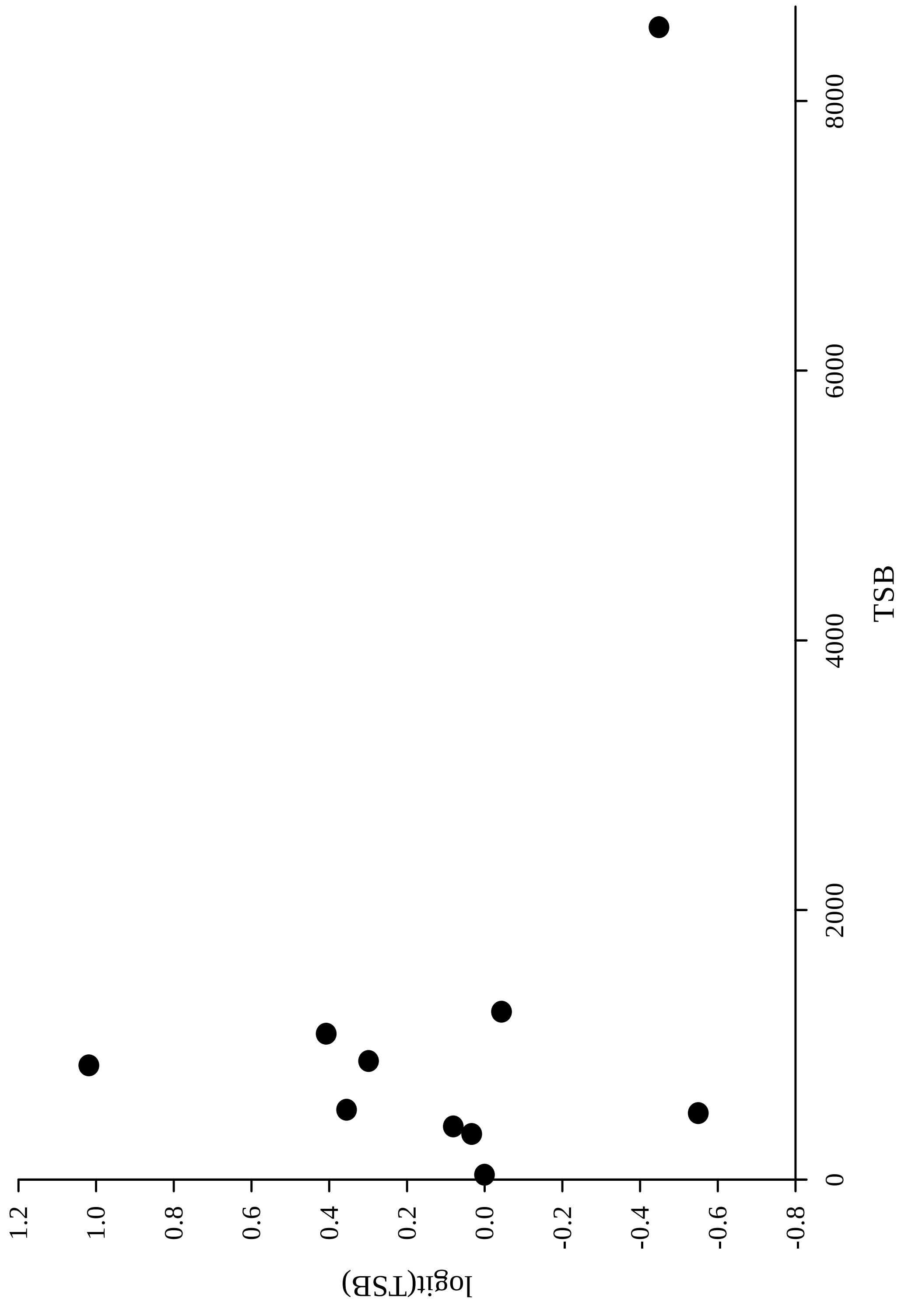
Study location	Proportion of birds surviving a breeding season and hatching ≥ 1 nest[a]		Nest survival[b]	Source
	Female	Male		
Alabama	0.27	0.18	0.47	this study
Florida	0.72	0.14	0.45[c]	DeVos and Mueller 1993
Georgia	0.69	0.31	0.51	Burger et al. *unpublished data*
Iowa	0.76	0.21	0.55[c]	Suchy and Munkel 1993
Mississippi	0.22	0.25	0.38	Taylor and Burger 1997
Missouri	0.74	0.26	0.44	Burger et al. 1995
Oklahoma	0.68	0.20	0.48[c]	Cox et al. 2005

[a] Studies defined the end of the breeding season as 1 September with the exception of DeVos and Mueller (1993) which used 31 September and Cox et al. (2005) which used 15 September.

[b] Nest survival computed from daily survival rates for a 24-day incubation period.

[c] True nest survival expected to be lower because study used apparent nest survival as an estimator (Mayfield 1961).

Figure 1. Group smoothed plot of number of days since most recent prescribed fire (TSB), a continuous covariate, used in analyses of daily survival rate of Northern Bobwhite nests at Conecuh National Forest, AL, 2002-2004. Group smoothed plots represent the parametric form of a continuous covariate via a logit link with daily survival rate (DSR). Continuous covariates included in the logit are assumed to have a linear effect on DSR. This plot does not suggest a particular nonlinear relationship.


logit(TSB)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
TSB
0
2000
4000
6000
8000

III. NORTHERN BOBWHITES IN A FIRE-MAINTAINED LONGLEAF PINE LANDSCAPE: SURVIVAL COST OF INCREASED MOBILITY IN A VARIABLE ENVIRONMENT

Abstract.-Empirical data of variation in a species' demography as a response to change in its environment can provide tests of evolutionary hypotheses and increase efficacy of conservation efforts. I studied survival and movement of Northern Bobwhites (*Colinus virginianus*) in fire-maintained longleaf pine (*Pinus palustris*) forests in south-central Alabama. Bobwhite populations and extent of fire-maintained longleaf pine forest have been declining for at least the last 4 decades. I sought to understand how daily survival rates and daily movement rates vary with temporal aspects of prescribed fire (i.e., time since last burn and season of burn). I found daily survival of Bobwhites is most influenced by mean minimum distance moved per day and that increasing movement leads to decreased survival rates. In turn, daily mobility of Bobwhites varied with respect to time since last prescribed fire, season of year, and whether an individual was associated with a food plot or not. Daily mobility of Bobwhites was greatest immediately prior to (i.e., April to May) and during (i.e., May to September) the breeding season and was reduced during the remainder of the year. Our results provide support for a survival cost of increased mobility in Bobwhites. These findings indicate that longleaf pine

forests managed with growing season fire and provision of food plot areas interspersed within longleaf pine forests will lead to increased daily survival rates of Bobwhites.

INTRODUCTION

The demography of species in variable environments is a topic of theoretical (Clobert et al. 2001) and conservation (Beissinger 1995, Holt and Gomulkiewicz 2004) interest. Understanding how survival and fertility respond to a fluctuating environment can provide insights into evolution in variable environments (Roff 2005) and also can increase efficacy of conservation efforts. For example, conservation can benefit from knowledge of demography in variable environments when demographic stochasticity may lead to extirpation or extinction in these variable environments (Lande et al. 2003) or when anthropogenic sources will lead to changes in the magnitude and expectation of variation in an environment (Beissinger 1995).

Fire-maintained habitats are one such example of a variable, yet predictable, environment (Komarek 1964, Frost 1998). In North America, the longleaf pine (*Pinus palustris*) ecosystem is one of the most fire-prone regions where fires occurred naturally every 2-8 years (Frost 1998). Despite the diverse plant (Harcombe et al. 1993, Peet and Allard 1993) and animal (Folkerts et al. 1993, Guyer and Bailey 1993, Engstrom et al. 2005) communities, fire suppression and land conversion has resulted in only 5-7% of this ecosystem remaining in its former range from southeastern Virginia to eastern Texas along the Southeastern Coastal Plain (Frost 1993). Restoration and management of longleaf pine forests use frequent, repetitive prescribed fire (Glitzenstein et al. 1995). However, prescribed fire can be applied at different times of the year and with different annual frequencies. These attributes characterize the fire-mediated environmental variability encountered by species inhabiting fire-maintained longleaf pine forests (Robbins and Myers 1992).

The influence of season and frequency of prescribed fire on avian species in longleaf pine forests has previously been reported, although this has mostly been restricted to inference concerning changes in avian community composition and abundance of particular species (review in Engstrom et al. 2005). In general, these studies suggest that bird communities may be affected by season of fire, but certain species appear to require frequent fire to persist in longleaf pine forests (Engstrom et al. 2005). While studies of this type may be informative for coarse landscape level effects of prescribed fire, detailed information on the demography of a species is required for conservation efforts to be maximally effective (van Horne 1983, Holmes et al. 1996).

In this study, I investigate how temporal aspects of prescribed fire (i.e., season of burn and time since burn) influence demographic attributes of a common avian species, Northern Bobwhites (*Colinus virginianus*; hereafter Bobwhites), in longleaf pine forests. The Bobwhite is a small gallinaceous species (178 g, Brennan 1999) that inhabits early successional habitats in eastern U. S. and northeastern Mexico (Brennan 1999). Bobwhite populations have declined throughout its geographic range since at least the 1960's (Brennan 1999). In the Southeast, fire-maintained savannas in pine forests, especially those in longleaf pine forests, represent a substantial portion of the Bobwhite's geographic range that could provide quality habitat (Dimmick et al. 2002). Although Bobwhites have been the focus of much fire-related research (e.g., Stoddard 1931) and Bobwhite populations increase with frequent, repetitive use of prescribed fire (Engstrom et al. 2005), little work has examined how demographic attributes of the species are related to temporal aspects of prescribed fire. Chapter II reported on Bobwhite nest success and female success in longleaf pine forests managed with prescribed fire. In this paper I focus on survival and movement of Bobwhites throughout the annual cycle in relation to temporal aspects of prescribed fire.

Our objective in this study was twofold. First, I sought to document daily survival rates of Northern Bobwhites in fire-maintained longleaf pine forests. Further, I sought to develop inference pertaining to the individual, temporal, and environmental factors (i.e., covariates) that may explain heterogeneity in survival rates based on *a priori* models, which represented alternative hypotheses. Pertaining to this first objective, I also sought to evaluate how daily mobility of Bobwhites may influence survival. Numerous theoretical studies have suggested (reviewed in Clobert et al. 2001) and some empirical investigations have demonstrated (e.g., Yoder et al. 2004) a survival cost for increased mobility or dispersal. Second, where daily measures of Bobwhite mobility had substantial influence on daily survival rate, I examined patterns in mobility associated with individual, temporal, and environmental covariates. Based on results of survival and movement analyses, I discuss results in the context of Bobwhite ecology and theoretical models of population dynamics in variable environments. I also discuss conservation implications of these findings.

STUDY AREA AND METHODS

I studied Northern Bobwhites at Conecuh National Forest (CNF) in Covington and Escambia counties, Alabama (31.1°N, 86.6°W). CNF is located in the Southeastern Coastal Plain physiographic region and covers nearly 340 km^2, of which approximately 110 km^2 is mature longleaf pine and mixed pine-hardwood forests. Longleaf pine forests in CNF are classified as the following landtype associations: Pine Hill, Dougherty Plain, and Wet Pine Flatwoods (Carter et al. 1999). The understory plant community contains shrubby and herbaceous vegetation typical of longleaf pine forests (Carter et al. 1999). Historically, few longleaf pine forests in this region were converted to agricultural uses, and thus many native understory species still persist (e.g., wiregrass [*Aristida* spp.]; Croker 1987). CNF is managed by the US Forest Service with triennial prescribed fire during either the growing (mid-March to early September) or dormant (mid-September to early March; Robbins and Myers 1992) seasons. Private lands within CNF are primarily longleaf pine and mixed pine-hardwood forests, yet are rarely burned (*T. H. Folk, personal observation*).

FIELD METHODOLOGY

I captured Bobwhites with welded wire funnel traps in February, March, May, and October from February 2002 to May 2004. Additional individuals also were captured by netting roosting coveys (October to March) where ≥ 1 individual was radiomarked (Truitt and Dailey 2000). Captured Bobwhites were sexed, aged, weighed to the nearest 2 g with a Pesola Spring scale, marked with a uniquely numbered leg band (size 7, National Band and Tag Co., Newport, Kentucky, USA), and equipped with a necklace-style radiotransmitter (model A3900, Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA). Subadults hatched the previous breeding season prior to radio attachment while adults hatched >1 breeding season prior to radio attachment (Brennan 1999).

Transmitters weighed approximately 6.3 g, had a life expectancy of 300 days, and were equipped with a 4-h mortality switch. Transmitters were not attached to individuals weighing < 125 g. Because several studies suggest that radiotransmitters themselves do not influence survival or body mass dynamics of Bobwhites (reviewed in Folk et al. *in review*), I did not use an acclimatization period before recording telemetry locations. Instead, I did not collect radio locations for radiomarked individuals (both recently marked birds and Bobwhites radiomarked prior to the trapping period) when associated with an active trap site (i.e., recently baited location). Trapped Bobwhites would remain near active trap sites after radio attachment and habitual use of the trap site may have increased probability of detection by predators (*T. H. Folk personal observation*). Traps and bait were removed from a location after either the majority of a presumed 10-12 bird covey was trapped or 4-5 days after the first Bobwhite was radiomarked, whichever came first.

Radiomarked individuals were located ≥ 5 times week^{-1} during the majority of the annual cycle (i.e., February to September), and ≥ 4 times week^{-1} during the remainder of the year (i.e., October to January). Estimated locations of radiomarked birds were determined with Lenth's (1981) maximum likelihood estimator in SAS (SAS Institute Inc. 2004) from triangulation data. Estimated radio locations (hereafter locations) where the error ellipse was > 5000 m^2 were excluded from analysis.

At each location, I classified the individual as alive or dead based on the presence or absence of the mortality radio signal. I measured the Euclidean distance between sequential locations for each individual. To estimate mean minimum daily movement, I divided the measured Euclidean distance between two sequential locations by the number of days elapsed between the locations (i.e., exposure interval).

COVARIATE DEVELOPMENT

I sought to explain heterogeneity in daily survival rate and daily movement rate (DMR) of radiomarked Bobwhites with covariates related to individual, temporal, or environmental phenomena. Incorporation of covariates into models of population parameters acts to increase precision of parameter estimates and reveal important ecological relationships between covariates and the estimated parameters (Pollock 2002).

Individual covariates in models of DSR include age (AGE) and sex (SEX) of the radiomarked individual and an estimate of the mean minimum daily movement distance (DIST). AGE and DIST were time-variant covariates (Table 1). Subadults surviving past 1 September in the year after hatch were reclassified as adults on 2 September. DIST was calculated for each location. AGE, SEX, and DIST were covariates in analysis of DSR, and AGE and SEX were used as covariates in models of DMR. DIST became the response variable for models of DMR. Inclusion of AGE and SEX in models of DSR and DMR allowed evaluation of age- and sex-specific variation in demography, which can reveal important aspects of a species' life history (Stearns 1992). In general, I predicted subadults to have lower survival and increased mobility as compared to adults. This reflects age-related patterns in, for example, efficacy of predator avoidance and knowledge of resources and dispersal processes. Bobwhite mortality can also vary with respect to intra-annual sex-related patterns in susceptibility to predation (e.g., males singing at exposed perch sites prior to the breeding season, females depredated during breeding season as a result of incubation or brood rearing activities; Burger et al. 1995). Use of DIST as a covariate in DSR models allowed evaluation of the potential cost of increased mobility (Yoder et al. 2004). I predicted DSR would decrease with increasing DIST, and in turn, I predicted DMR would vary intra-annually as compared to other sources of heterogeneity.

Temporal covariates used in models of DSR and DMR represent hypothesized patterns in heterogeneity that are not explicitly identified in individual or environmental covariates. Two temporal covariates (COVEY and SEASON) described intra-annual variation in DSR and DMR. Individuals were classified on each observation by COVEY and SEASON based on date. COVEY reflected within year differences in the sociobiology of Bobwhites; namely whether individuals were in coveys (2 October to 7 April) or not (8 April to 1 October). SEASON reflected both sociobiological and reproductive differences in the annual cycle, and are defined as the covey period (2

October to 7 April), prenest period (8 April to 21 May), nesting period (22 May to 1 September), and postnest period (2 September to 1 October). Definition of time periods for COVEY and SEASON are based on observations of radiomarked Bobwhites at CNF by the senior author. Both COVEY and SEASON were used as covariates in models of DSR and DMR.

Fire causes initially rapid changes in resources (e.g., removal of protective cover, increased food supplies by removal of ground litter), but plant succession after a fire leads to gradual shifts in those resources (e.g., protective cover regenerates, increased ground litter limits availability of seeds in ground layer). To describe this temporal post-fire pattern I developed two similar, yet subtly different, temporal covariates. First, DSLB describes the total number of days since the most recent prescribed fire, while GSDSLB describes the number of growing season days, where the growing season is 1 April to 1 September, since the most recent prescribed fire. DSLB and GSDSLB were both used as covariates in models of DSR and DMR. I anticipated DSR to increase initially with increasing GSDSLB and DSLB and then decline as those covariates extended beyond the window of a normal fire interval (i.e., 2-3 years). I similarly expected DMR to be greatest for low levels of GSDSLB and DSLB, decline to some intermediate value (i.e., 2-3 years), and then increase as areas approach an unburned state.

I developed a suite of environmental covariates to describe variation in habitats due to fire history and vegetation type. BURN describes areas as either subject to repeated prescribed fire or whether fire had been suppressed in an area. There is consistent evidence that repeated fire is beneficial to Bobwhite populations (Engstrom et al. 2005). I included it as a covariate to quantify the magnitude of difference in survival and movement between burned and unburned areas. In a slightly different context, I next wanted to examine the magnitude of difference in survival and movement attributable to season of burn. BURNSEASON more explicitly described burn history: areas were classified as having burned most recently during the growing season (1 April to 1 September), dormant season (2 September to 31 March), or were unburned. The influence of season of burn on vegetative structure of longleaf pine forests is not realized after a single fire (Robbins and Myers 1992). Rather, it requires repeated application during either the growing or dormant season to produce forests with different vegetative composition and structure. Burn records were not sufficiently complete for CNF to construct a better proxy for fire history that, for example, reflected the number of growing season fires in the recent past. However, land management at CNF is principally driven by development and maintenance of suitable habitat for the endangered red-cockaded woodpecker (*Picoides borealis*). This species prefers areas where woody vegetation in the midstory is minimal and the understory contains primarily herbaceous and shrubby plant species (Rudolph et al. 2002). These are conditions created by repeated growing season fire (Robbins and Myers 1992), and CNF staff prioritizes these areas for prescribed burns during the growing season. Remaining areas are burned during the dormant season. Thus, if an area is classified as having burned during the growing season there is a high probability that it has a history of repeated growing season fire, and the converse for areas classified as having been burned during the dormant season.

Planting and maintenance of food plots (i.e., areas planted with plant species that provide food and cover for a target species) is a common management strategy for Bobwhites, yet these areas can also receive a disproportionate higher harvest pressure than the rest of the landscape. Alternatively, these areas may provide suitable enough resources to reduce mobility of individuals. To evaluate whether food plots decreased DSR and DMR, covariate FOOD describes whether locations were in or near (i.e., within 100 m) an actively maintained food plot or not. TIMBER indicated the timber type (i.e., pine, pine-hardwood, upland hardwoods, bottomland hardwoods, or miscellaneous areas [e.g., food plot, clearcut, areas directly adjacent to human development, etc.]) at each location. Timber type classification was obtained from GIS layers developed by the USFS for CNF. Private property was digitized and classified according to USFS criteria.

MODEL DEVELOPMENT

I developed *a priori* models of DSR and DMR based on previously tested hypotheses in the literature and novel ideas based on field observations. Because the potential covariate list was extensive and I wished to only consider biologically plausible and interpretable models, I constrained model development according to the following criteria:

1. Models were composed of ≤ 4 covariates and these covariates contained ≤ 2 sources of DSR or DMR heterogeneity (i.e., individual, temporal, and environmental). These restrictions helped ensure that a candidate model was

interpretable and thus useful in developing inference about heterogeneity in DSR and DMR.

2. Several groups of covariates (i.e., BURN, BURNSEASON, GSDSLB, and DSLB; FOOD and TIMBER; COVEY and SEASON) represented alternative hypotheses relating to the pattern of influence of a particular covariate. For example, COVEY and SEASON suggest that the response variable may vary most appreciably over either 2 or 4 intra-annual time periods, respectively. Because of the alternative nature of these sets of covariates, I did not develop models where more than one covariate from a group appeared in a model.
3. I limited interactions in models of DSR and DMR to age and sex (i.e., AGE*SEX), sex and discrete intra-annual variation (i.e., SEX*COVEY or SEX*SEASON), age and discrete intra-annual variation (i.e., AGE*COVEY or AGE*SEASON), and intra-annual variation across calendar year (i.e., SEASON*YEAR or COVEY*YEAR).

Under these criteria, I developed 272 models of DSR and 193 models of DMR. I assume that covariates measured at time *t* influenced the fate observed at time *t*, while distance traveled between time *t* and *t*+1 was influenced by covariates of the location at time *t*. The latter reflects our hypothesis that movement was most influenced by conditions at the point of origin rather than conditions at the destination.

I used generalized non-linear models with a binomial likelihood to model variation in DSR as a function of individual, temporal, and environmental covariates. This approach builds on the model of Bart and Robson (1982) and is described more fully in Rotella et al. (2004). *A priori* models of DSR were incorporated into the binomial likelihood via a logit link function (Hosmer and Lemeshow 2000). Maximum likelihood estimates (MLEs) of parameters in models of DSR were obtained with PROC NLMIXED in SAS, although random effects were not incorporated into models considered here. I used the Newton-Raphson Method with Ridging optimization algorithm to obtain MLEs of parameters, and their standard errors, in models of DSR.

I evaluated model adequacy at 2 steps in the analysis. First, I evaluated model fit from the global model (i.e., the most highly parameterized model) before fitting any *a priori* models of DSR. Second, after fitting and ranking *a priori* models of DSR, I evaluated model adequacy of DSR models deemed best given our information theoretic approach to model selection. Model fit at both steps was assessed with the test described by Hosmer and Lemeshow (1980). Pigeon and Heyse (1999) and Kuss (2002) suggested this test may not be appropriate when continuous covariates are used; however, our sample sizes were large and this reduces the bias associated with incorporation of continuous covariates (Kuss 2002).

I derive inference in two ways from models of DSR. First, I compute DSR (and their associated 95% CI) for comparison with other estimates of DSR in the literature.

Second, I compute odds ratios for parameters appearing in the best model(s). Odds ratios evaluate the likelihood for survival over a single day of individuals in a *comparison state* (e.g., subadults) to individuals in the *reference state* (e.g., adults). Odds ratios (and their associated 95% CI) were computed according to Hosmer and Lemeshow (2000). All odds ratios were computed from model averaged beta values using unconditional standard errors because uncertainty existed in model selection (see *Model Selection and Inference* below for details on model averaging and uncertainty).

MODELS OF DAILY MOVEMENT RATE OF NORTHERN BOBWHITES

I modeled DMR of Bobwhites as a process following a Weibull distribution. I was motivated to select the Weibull distribution to describe daily movement for several reasons. First, inference on estimated attributes of a Weibull distribution is well developed (Hougaard 2000, Lawless 2003). Second, the Weibull distribution is capable of describing data with normal and negative exponential distributions (Tufto et al. 1997), thus reducing model selection bias associated with distributional misspecification (Fishler et al. 2002). Third, the Weibull distribution is seeing increasing use in ecological studies (e.g., Pinder et al. 1978, Ricklefs 1998, Brøseth et al. 2005, Tufto et al. 2005) and estimation of parameters in a Weibull distribution for movement relate to theoretical aspects of dispersal (i.e., standard deviation in dispersal distances; Tufto et al. 1997). Finally, obtaining parameter estimates in the Weibull distribution via maximum likelihood techniques is easily achieved (Bailey and Dell 1973, Lawless 2003).

Daily movement rate of radiomarked Bobwhites was modeled using a 2-parameter Weibull distribution where the probability distribution function for uncensored data takes the form

$$f(DIST) = (\tau / \gamma)(DIST / \gamma)^{\tau - 1} \exp(-(DIST / \gamma)^{\tau})$$

and *DIST* is the observed mean minimum daily movement distance, γ is the scale parameter, and τ is the shape parameter (Hastings and Peacock 1975). In the context of survival data modeled with the Weibull distribution, the shape parameter is most closely related to the hazard function and describes changes in the instantaneous mortality rate at time *t* (Lawless 2003). In the context of daily movement distances, I interpret this *hazard function* to evaluate the probability of daily movement across the sampled population. When the shape parameter is near 1.0, the hazard rate (i.e., probability of movement) can be considered constant over time. Preliminary analyses suggested a shape parameter near 1.0 in our data; thus, I did not consider modeling DMR as a function of covariates via a link function describing the shape parameter. Instead, the scale parameter more closely relates to the distribution of observed response data values (i.e., mean minimum daily distance moved). In the context of describing movement data, I was most interested in the relationship between covariates in *a priori* models and the variation in mean minimum daily distance moved. Thus, I incorporated *a priori* models of DMR into the Weibull likelihood function by relating γ and covariates with an identity link function (Lawless 2003). Convergence to maximum likelihood estimates was achieved with the log-likelihood form of the Weibull probability density function using the Double Dog-leg algorithm described by Dennis and Mei (1979).

I assessed model fit in a post hoc approach. Burnham and Anderson (2002) suggest evaluation of model fit with a global model prior to model selection. In the context of nonlinear regression, use of a global model assumes identical distribution of errors across all levels and failure to meet these assumptions result in biased MLEs (Motulsky and Christopoulos 2004). Based on the number of covariates incorporated into models of DMR I felt this assumption was not valid. Instead, I evaluated the appropriateness of the Weibull distribution to describe movement data with Q-Q plots for categorical levels described by the information theoretic best model(s) selected (Lawless 2003).

I derive inference from regression models in the Weibull likelihood on the predicted mean minimum daily distance moved which is computed per level of a model. Mean distance moved estimated by *a priori* model *k* at the *i*th level of the covariates is given as

$$\overline{\mathrm{X}}_i^k = (\mathbf{x}\beta_i^k)(\Gamma[(\tau^k + 1)/\tau^k])$$

where τ^k is the MLE for the shape parameter for model *k*, β_i^k are MLEs for covariates in model *k* at the *i*th observed level, and $\Gamma(x)$ is the standard gamma function (Hougaard 2000) defined as

$$\Gamma(x) = \int_0^\infty u^{x-1} e^{-u} du \qquad z > 0.$$

EVALUATION OF LINEARITY IN CONTINUOUS COVARIATES

Continuous covariates were used in models of DSR (i.e., GSDSLB, DIST, and DSLB) and DMR (i.e., GSDSLB and DSLB). The incorporation of continuous covariates into the logit and identity link functions assumes a linear effect between the covariate and the response variable (Hosmer and Lemeshow 2000). Hosmer and Lemeshow (2000: 99) suggest the use of *group smoothed plots* to evaluate this assumption of linearity. In this procedure, I ranked the observed values for a particular continuous covariate by magnitude and categorized observations by deciles. I then created a 10-level categorical variable to describe classification of the continuous covariate into deciles. The continuous covariate was replaced with its categorical representation in the AIC (for models of DSR) or SIC (for models of DMR) best model for the particular covariate. Maximum likelihood estimates of model parameters were then recalculated. A group smoothed plot is then developed from the resulting beta values for the categorical variable and midpoints of each decile. The plotted points should be nearly linear if the assumption of linearity in a continuous covariate is appropriate. If the plotted points are not linear, the parametric form of the continuous covariate (e.g., quadratic, sigmoid, etc.) will be discernable from the plot. Parameter transformations were done in Sigmaplot®. The final candidate set of *a priori* models for DSR and DMR are those where continuous covariate(s) is of the appropriate form suggested by group smoothed plots.

INFORMATION THEORETIC MODEL SELECTION AND INFERENCE

I conducted separate information theoretic model selection procedures for models of DSR and DMR. Our objective with DSR models was twofold in that I wanted to select model(s) for prediction of parameters for use in population models and select model(s) to understand heterogeneity in DSR of radiomarked Bobwhites. Because of these criteria I selected Akaike's Information Criterion (AIC; Akaike 1973) for model selection in analyses of DSR (Taper 2004). Our objective with DMR models was to develop a better understanding of daily movement rates of radiomarked Bobwhites. For this reason I selected Schwarz's Information Criterion (SIC; Schwarz 1978) for model selection in analyses of DMR. AIC is a model selection tool that minimizes the Kullback-Leibler information (Burnham and Anderson 2002). This approach is most appropriate when selected models will be used for predictive purposes. In contrast, SIC is in the class of order consistent information criteria in that it balances the principle of parsimony to derive the true dimension of the phenomenon with the complexity of the sample size from which inference will be drawn (Taper 2004). Further, AIC may not appropriate when *a priori* models can not be considered nested within one of the candidate models (Takeuchi 1983, Murata et al. 1994, Sugiyama and Ogawa 2001), which occurred in models of DMR (see above *Models of Daily Movement Rate of Northern Bobwhites*). While I modeled Bobwhite daily mobility with the Weibull distribution, daily mobility data has also been modeled with a negative exponential distribution (e.g., Kuras et al. 2003); however, Fishler et al. (2002) found SIC to be robust in the presence of distributional misspecification.

Within DSR or DMR analyses, model comparisons were made with Δ_i, which is the difference between the information criterion (IC) value for model i and the lowest observed IC value among the candidate set of models. Models with $\Delta_i < 2$ are considered to have substantial support given the data. For models of DSR, I also computed the Akaike weight per model which reflects the relative likelihood of the model given the data and the candidate model set (Burnham and Anderson 2002). I did not use Sugiura's (1978) Second-Order form of AIC (frequently referred to as *small sample AIC*; Burnham and Anderson [2002]) in analysis of DSR because the ratio of sample size to maximum number of parameters was large. In models of DSR, inferential parameters (e.g., odds ratios) came from the AIC best model (i.e., $\Delta_i = 0$) if little uncertainty existed in model selection (i.e., Akaike weight > 0.90 for AIC best model). If uncertainty did exist, inference came from across all models with model averaged parameters and unconditional standard errors (Burnham and Anderson 2002). Estimates of DSR were derived from model averaged betas values for the covariates with substantial support (i.e., Akaike weights > 0.38; White and Burnham 2005). I calculated the relative importance of a covariate by summing the Akaike weights for models that contain that covariate. Covariates that explain considerable heterogeneity in DSR will have a low AIC value and thus high Akaike weights. Model selection with SIC follows similarly from AIC with the exception that SIC is computed as

$$\mathrm{SIC} = -2\ \mathrm{Log}(\mathcal{L}) + \mathrm{Log}\ (n)K$$

where n is the sample size used to evaluate the likelihood function and K is the number of estimated parameters in the likelihood function for a particular model. I did not compute model averaged estimates from models of DMR even if model selection ambiguity occurred. Deriving model averaged parameters estimates when nonlinear, structural parameters are being considered (i.e., τ) is not appropriate (Burnham and Anderson 2002). All summary values are reported with the associated ± SE unless indicated otherwise. All analyses were done with SAS (SAS Institute 2004).

RESULTS

I monitored 319 radiotagged Bobwhites (97 subadult females, 111 subadult males, 49 adult females, 62 adult males) between 2 March 2002 and 3 September 2004. Mortality was recorded for 245 radiomarked individuals during the course of study; 60 were right-censored presumably due to transmitter failure; and 14 were alive at the end of the study period. I recorded 20,396 radio locations for Bobwhites. Nearly all locations (95.6%, n = 19,494) were recorded over an exposure interval of ≤ 3 days, and 73.4% (n = 14970) were recorded over an exposure interval of 1 day.

MODELS OF DAILY SURVIVAL RATE OF NORTHERN BOBWHITES

I used 3 continuous covariates in models of DSR: GSDSLB, DIST, and DSLB. A group smoothed plot for DIST supported a logit-linear relationship, and suggested the relationship between DIST and DSR was negative (Fig. 1*a*). Logit-linear relationships for DSLB (Fig. 1*b*) and GSDSLB (Fig. 1*c*) were more ambiguous although alternative parametric forms were not obvious. I did not transform continuous covariates in the logit for DSR and *a priori* candidate models reflect a logit-linear relationship for GSDSLB, DIST, and DSLB. Tests of model adequacy suggest the global model adequately describes the data ($\chi^2 = 5.06$, df = 8, $P = 0.75$) and all AIC best models (i.e., models with ΔAIC < 2) also adequately described the data (all *P*'s > 0.44).

Model ranking by AIC value indicated 3 models with substantial support given the data (Table 2). The model with the lowest AIC score included additive effects of AGE, BURNSEASON, DIST, and TIMBER. BURNSEASON and DIST were common to all AIC best models. AGE and TIMBER were common to two of the three AIC best models. The Akaike model weights for the AIC best model was less than 0.90 and indicated uncertainty in model selection results. I computed model averaged parameter estimates and base inference on these results.

Four covariates appear to have substantial importance for explaining heterogeneity in DSR of Bobwhites: DIST, BURNSEASON, AGE, and TIMBER (Table 3). The odds ratio for AGE of Bobwhites indicated that adults were 1.267 (1.014-1.582 95% CI) times more likely to survive each day than subadults. Although BURNSEASON appeared to be an influential parameter in DSR (Table 3), odds ratios indicate DSR varies most appreciably in longleaf pine forests managed with growing season prescribed fire than unburned or longleaf pine forests managed with dormant season prescribed fire. Bobwhites in longleaf pine forests managed with growing season prescribed fire were 1.508 (1.138-2.000 95% CI) more likely to survive each day than individuals in longleaf pine forests managed with dormant season prescribed fire (Table 4).

DSR declines with increasing mobility (Fig. 2). Bobwhites that move 890 m in a day are twice as likely to die as compared to an individual that does not move in a single day. Several differences in DSR by TIMBER also are indicated by odds ratios (Table 5). Bobwhites in pine forests were more likely to survive than individuals in pine-hardwood and bottomland hardwoods. Similarly, Bobwhites in food plots, etc. are more likely to have a higher DSR than individuals in pine-hardwood and bottomland hardwoods (Fig. 3). DSR of Bobwhites in bottomland hardwoods is more likely to be lower than individuals in all other timber types except pine-hardwood forests. Model averaged betas (unconditional SE) are given for the following covariates: growing season burn = 0.3192 (0.1865), dormant season burn = -0.0918 (0.1539); adult = 0.2365 (0.1134) with subadults described by the reference condition (i.e., lack of a beta value for the condition); mean minimum daily distance moved = -0.0008 (0.0002); and covey = -0.3072 (0.0154), prenest = -0.3576 (0.0160), nest = -0.5759 (0.0146), and the covey period described by the reference condition.

I used 2 continuous covariates in models of DMR: DSLB and GSDSLB. The relationship between DSLB and DMR approximated a negative exponential (Fig. 4*a*), which we transformed as:

$$\text{DSLB}_{\text{transformed}} = -6.376 + (40.025 * 586.521)/(586.521 + \text{DSLB}_{\text{untransformed}}).$$

A linear relationship existed between GSDSLB and DMR (Fig. 4*b*). Results reflect the use of transformed values of DSLB in all *a priori* models of DMR.

Two models ranked best in analyses of DMR (Table 2). Both models indicated heterogeneity in DMR was explained by SEASON*YEAR and FOOD. The SIC best model (i.e., $\Delta_i = 0$) also had the effect of GSDSLB while the second SIC best model (i.e., $\Delta_i = 0.84$) had the effect of DSLB. The third best model was 11.22 SIC units away from the SIC best model. I assessed goodness-of-fit of Weibull regression models by visual inspection of Q-Q plots. Inspection of these plots for the two SIC best models did not suggest lack of fit for either model (Fig. 5*a*,*b*).

Mobility varied across season and years, and was lower for individuals in the vicinity of a food plot. Of the seasons, individuals were most mobile in the prenest period and least mobile during the postnest period (Fig. 6). Mobility during the nesting and covey periods were similar to each other and appeared intermediate to mobility during prenest and postnest. Daily mobility declined with increasing time since burn in both GSDSLB and DSLB.

DISCUSSION

SURVIVAL COST OF INCREASED MOBILITY IN NORTHERN BOBWHITES

Numerous theoretical evolutionary models of dispersal suggest that costs exist for dispersing individuals as compared to philopatric ones (reviewed in Clobert et al. 2001). These costs can include diminished reproductive opportunities (Danchin and Cam 2001), but more commonly referenced is decreased survival for more mobile dispersers as compared to less mobile philopatric individuals. The likelihood of mortality for dispersers can be heightened due to unfamiliarity with surrounding habitats (Greenwood and Harvey 1982, Yoder et al. 2004) or increased activity that may attract predators (Lima 1998). Our findings provide consistent and substantial support for a survival cost for increased mobility in Bobwhites. Individuals whose daily movement rate was in excess of 890 m were at least twice as likely to perish as compared to an individual that did not move; however, the majority of daily movement distances (n = 20131 of 20396 observations) were < 890 m. Therefore, while long distance daily movements are rare, they pose a substantial survival cost to Bobwhites.

Beyond the establishment of a survival cost for increased mobility in Bobwhites, it is also of interest to understand whether this cost is caused by unfamiliarity with surroundings or increased activity that may attract predators. Yoder et al. (2004), for example, demonstrated that survival cost for increased mobility in Ruffed Grouse (*Bonasa umbellus*) was attributable more to reduced site familiarity in mobile individuals than attraction of predators. A bimodal pattern should be obvious in the group smoothed plot (i.e., modes corresponding to individuals in familiar and unfamiliar habitats) if the survival cost of mobility in Bobwhites was driven by low site familiarity more so than increased activity level. Examination of group smoothed plots for DIST in models of DSR (Fig. 1*a*) does not reveal a distinctly nonlinear pattern between the effects of mobility on Bobwhite DSR. The dichotomy between survival costs of mobility due to site familiarity or increased activity levels may vary with different landscape contexts.

The influence of mobility on survival in gallinaceous species has been addressed by several other studies, but lead to equivocal patterns. For example, no evidence for decreased survival has been demonstrated in dispersing Spruce Grouse (*Falcipennis canadensis*; Beaudette and Keppie 1992), Blue Grouse (*Dendragapus obscurus*; Hines 1986), Willow Ptarmigan (*Lagopus lagopus*; Schieck and Hannon 1989), and Ruffed Grouse (Small et al. 1993); however, Yoder et al. (2004) documented a survival cost for more mobile Ruffed Grouse. For Bobwhites in particular, Townsend et al. (2003) did not document a survival cost during the breeding season after the dispersal event for Bobwhites classified as dispersers whereas Williams et al. (1998) did document a survival cost in winter for individuals in more mobile coveys. This is the first study to evaluate the survival cost of increased mobility in Bobwhites throughout the annual cycle. Disparate patterns in the relation of mobility and survival likely vary intra-specifically with different landscape contexts and inter-specifically with different life history strategies. Beyond establishment of a survival cost for increased mobility, studies should consider these intra- and inter-specific sources of heterogeneity.

FACTORS INFLUENCING MOBILITY OF NORTHERN BOBWHITES

Given that mobility appears to influence survival of certain species, it is also of interest to understand the factors responsible for increased mobility within species (Denno et al. 1996, Donahue et al. 2003). Examination of potential factors influential in mobility/dispersal will provide empirical tests of theoretical models of dispersal (Travis and Dytham 1999) and increase efficacy of conservation efforts (Holt and Gomulkiewicz 2004), especially if increased mobility poses a survival cost. Analysis of daily movement rate of Bobwhites at CNF indicated that two temporal factors (SEASON*YEAR, GSDSLB or DSLB) and one environmental factor (FOOD) explained the most heterogeneity in Bobwhite DMR (Table 2). Individual covariates (i.e., AGE and SEX) explained little of the heterogeneity in Bobwhite DMR.

Bobwhite daily mobility varied throughout the year with increases in daily mobility in prenest and nest period and decreased daily mobility in postnest and covey periods (Fig. 6). This pattern was consistent within a year, yet the magnitude of daily mobility within a season varied across the 3 years of study. Increased mobility prior to and during the breeding season may be associated with individuals roaming to find mates or suitable nest sites (e.g., Townsend et al. 2003). For example, Badyaev et al. (1996) documented increased nest success for female Eastern Wild Turkeys (Meleagris gallopavo) that sampled more habitats during a period before nesting. Future work should also better evaluate why this pattern in seasonal mobility may vary across years.

I also hypothesized that Bobwhite daily mobility would increase immediately after a fire, decrease with increasing time since burn as vegetative recovery provides quality habitat, and then again increase as time since burn approached unburned conditions (i.e., time since burn > 2-3 years). This would reflect Bobwhites preference for areas with greater overhead cover that provided protection from predators (Kohlmann and Risenhoover 1996). I found limited evidence of this hypothesized relationship in SIC best models of DMR. GSDSLB and DSLB were included in both SIC best models and Bobwhite DMR declined with increasing time since burn (reflected in GSDSLB and DSLB). I had, however, hypothesized that Bobwhite mobility would increase as time since burn approached unburned conditions. This hypothesis was built on the assumption that unburned habitats would not suit Bobwhite life history requirements and individuals would relocate to find more suitable areas. I did not find evidence for this relationship. The demographic dynamics of a Bobwhite population in deteriorating habitat is unknown, but populations decline without the presence of habitat disturbance (Brennan 1999). This result suggests that Bobwhite populations in habitats without prescribed fire may not disperse to more suitable, frequently burned habitat. Future work should more thoroughly investigate the evolutionary and conservation significance of a species' demographic response in deteriorating habitat.

Beyond the influence of daily mobility on Bobwhite survival, I documented heterogeneity in daily survival with respect to individual (i.e., AGE) and environmental (i.e., BURNSEASON and TIMBER) covariates. Little heterogeneity was explained by temporal covariates (Table 3). Bobwhite DSR was highest for adults in longleaf pine forests managed with growing season prescribed fire, and lowest for subadults in bottomland hardwood areas subject to dormant season prescribed fire (Tables 4 and 5).

Age-specific variation in demography is characteristic of many short-lived species of birds (Sæther and Bakke 2000, Bennett and Owens 2002); although, evidence of age-specific differences in survival rates of Bobwhites is ambiguous. Studies have documented increasing survival with age (this study, Cook 2004) or no influence of age on survival (Burger et al. 1995, Burger et al. 1998, Taylor et al. 2000, Townsend et al. 2003, Cox et al. 2004). Adults in this study were 1.267 times more likely to survive each day than were subadults. Researchers documenting age-related patterns in survival (especially when survival increases with age) attribute this pattern to age-related cognitive ability (i.e., older individuals are better able to select areas leading increased survival and reproductive performance). The seeming equivocal nature of age-related differences in Bobwhite survival may reflect the presence of certain factors influencing survival at variable times in the life cycle. For example, most of the studies mentioned previously (including this one) only document survival of Bobwhites after the age of 3-4 months. This selective approach is due to the inability to monitor very young Bobwhites.

Given this methodological restriction, age related patterns in survival may not be detected if they only occur immediately after hatch. Future work should begin to evaluate patterns in survival probabilities across the lifespan of Bobwhites.

I documented higher survival rates in longleaf pine forests managed with growing season prescribed fire as compared to longleaf pine forests managed dormant season prescribed fire. Bobwhite daily survival rates in unburned habitats was intermediate to those documented to longleaf pine forests managed with growing or dormant season prescribed fire. Unburned areas represented a variety of habitat conditions including areas surrounding agriculture, development, etc. As mentioned previously, the influence of season of fire on vegetative structure and composition is not realized with a single prescribed fire. Rather, repeated fire during a particular season must be used to produce different vegetative conditions. In general, forests managed with prescribed fire during the dormant season have less abundant herbaceous and shrubby vegetation in the understory, which is partly attributable to broad-leaved hardwoods in the midstory that produce shade on the forest floor (Waldrop et al. 1992). In contrast, areas burned repeatedly during the growing season have a greater abundance of herbaceous and shrubby plant species in the understory (Robbins and Myers 1992). Conditions in the latter burn state are more analogous to those preferred by Bobwhites (Kohlmann and Risenhoover 1996). Most studies in the longleaf pine ecosystem that have evaluated the influence of season of fire on bird species have primarily assessed change in community composition or abundance (Engstrom et al. 2005, Chapter I, Tucker et al. *in press*). This study establishes a demographic consequence of different season of fire in longleaf pine forests.

CONSERVATION IMPLICATIONS OF NORTHERN BOBWHITE DEMOGRAPHY IN FIRE-MAINTAINED HABITATS AND FUTURE RESEARCH

Disturbance is a characteristic of many natural environments (Pickett and White 1985). Historically, anthropogenic management has placed emphasis on minimizing at worst or eliminating at best the occurrence of disturbances. Suppression of natural fires and elimination of prescribed fires in the fire-prone longleaf pine ecosystem is perhaps one of the best case studies of anthropogenic modification of natural disturbance regimes (Frost 1993). Increasingly, the benefits of disturbances that mimic natural ones are being demonstrated (reviewed in Robbins and Myers 1992). This study contributes to this knowledge by developing an understanding of the demographic consequences of variation in fire for Bobwhites.

For conservation to be maximally effective for a species inhabiting a variable environment like fire-maintained longleaf pine forests, conservation actions should reflect the dynamic relationship between a species' demography and its environment. Frequently management actions are based on the relationship of a single demographic parameter (e.g., nest success) to an attribute of the environment (e.g., vegetative characteristic of the environment). Our results demonstrate that for Bobwhites consideration of environmental characteristics that affect DSR may not lead to the most efficacious conservation strategy. I demonstrate that Bobwhite DSR is most appreciably influenced by extent of daily mobility. Thus, effective conservation strategies aimed at increasing survival must also consider factors influencing Bobwhite mobility.

Results of survival and movement analyses here might be interpreted to suggest paradoxical conservation measures. First, for example, I demonstrate that survival rate of Bobwhites consistently declined with increasing mobility (Fig. 2); thus conservation measures should seek to develop a landscape that minimizes Bobwhite mobility. In turn, analyses of Bobwhite mobility indicate a negative relationship between DMR and two measures of time since burn. This leads to an erroneous conclusion, based on general knowledge of Bobwhite life history, that areas should not be burned for > 5-6 years. Numerous presence-absence studies indicate that Bobwhite populations decline after 3-4 years post burn (review in Chapter I). The resolving factor in development of efficacious conservation measures from this study that are consistent with other studies of Bobwhite life history and prescribed fire can be found in the relationship of mobility to association with food plots and the influence of season of burn on Bobwhite survival. Bobwhite mobility was reduced by association with food plots and Bobwhite survival was depressed in unburned and areas managed with dormant season prescribed fire. In summary, results of this study suggest that longleaf pine forests managed with growing season prescribed fire and containing protected areas of vegetation (i.e., food plots) are management actions that will lead to increased survival of Bobwhites.

The influence of prescribed fire on an area can be complex depending on temporal attributes of fire occurrence, severity of fire, and attributes of the understory (e.g., moisture content in residual vegetation). This study examined demography of Bobwhites with respect to one of these factors: temporal aspects of fire. Future work should more fully examine these other attributes of fire with respect to demography of Bobwhites and other avian species endemic to longleaf pine ecosystem. Further, work is needed to develop a better understanding of the inter-relationship between spatial contexts of unburned and burned areas and the demography of Bobwhites.

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Table 1. Summary of individual, temporal, and environmental covariates used in analyses of daily survival rate (DSR) and daily movement rate (DMR) of Northern Bobwhites at Conecuh National Forest, AL, 2002-2004.

Covariate	Analysis	Description	Units
Individual			
AGE	DSR, DMR	subadult or adult	categorical
DIST	DSR	Euclidean distance between successive radio locations per individual that represent mean minimum daily distance moved	continuous (m)
SEX	DSR, DMR	male or female	categorical
Temporal			
COVEY	DSR, DMR	Radio location collected during period of year when birds were organized in coveys (2 October to 7 April) or not (8 April to 1 October)	categorical
GSDSLB	DSR, DMR	Days during the growing season (1 April to 1 September) elapsed between most recent prescribed fire and date of radio location	continuous (days)
DSLB	DSR, DMR	Days elapsed between most recent prescribed fire and date of radio location	continuous (days)
PFIRE	DMR	Daily probability of the occurrence of natural, lightning-ignited Fire	continuous (probability)
SEASON	DSR, DMR	Radio location collected during covey period (2 October to 7 April), prenest (8 April to 21 May), nest (22 May to 1 September), or postnest (2 September to 1 October)	categorical
Environmental			
BURN	DSR, DMR	Whether a forest had been burned within the last 10 years or not	categorical

BURNSEASON	DSR, DMR	Season of most recent prescribed fire of forest containing radio location: growing season, dormant season (2 September to 31 March) or unburned	categorical
FOOD	DSR, DMR	Whether a radio location was in or near (within 100 m) a food plot or not	categorical
TIMBER	DSR, DMR	Timber type of forest containing radio location: pine, pine-hardwood, upland hardwood, bottomland hardwood, or other (e.g., food plot, clearcut, etc.)	categorical

Table 2. Models of daily survival rate (DSR) and daily movement rate (DMR) of Northern Bobwhites at Conecuh National Forest, AL, 2002-2004. Models with ΔAIC < 4 (DSR models) and ΔSIC < 4 (DMR models) are presented. All models represent additive effects in the logit link (DSR models) or identity link (DMR models) unless indicated otherwise (i.e., covariate1*covariate2).

DSR models	Log($\mathcal{L}$)	Number of parameters	AIC	ΔAIC	Akaike weights
AGE BURNSEASON DIST TIMBER[a]	-1318.20	9	2654.40	0	0.22
AGE BURNSEASON DIST FOOD	-1321.98	6	2655.97	1.57	0.10
BURNSEASON DIST TIMBER	-1320.04	8	2656.08	1.68	0.09
AGE DIST TIMBER	-1321.40	7	2656.79	2.40	0.07
AGE BURNSEASON DIST	-1323.49	5	2656.97	2.57	0.06
BURNSEASON DIST FOOD	-1323.57	5	2657.15	2.75	0.05
BURNSEASON DIST SEX TIMBER	-1320.00	9	2658.01	3.61	0.04
BURNSEASON DIST	-1325.07	4	2658.13	3.7	0.03
DMR models	Log($\mathcal{L}$)	Number of parameters	SIC	ΔSIC	SIC weights
GSDSLB FOOD SEASON*YEAR	-121774.07	15	243696.99	0	0.60

DSLB FOOD SEASON*YEAR	-121774.49	15	243697.84	0.84	0.40

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[a] See Table 1 for description of covariates.

Table 3. Relative importance values of covariates used in models of Northern Bobwhite daily survival rate (DSR). A parameter's importance value is the sum of Akaike weights across models where that parameter occurs. Covariates where the relative importance value is > 0.38 are considered to have substantial support (White and Burnham 2005). DSR estimates reported in this study were derived from model averaged betas values for the covariates with substantial support.

Covariate	Relative importance of parameter
DIST[a]	0.998
BURNSEASON	0.623
AGE	0.615
TIMBER	0.489
FOOD	0.228
SEX	0.108
COVEY	0.083
BURN	0.080
GSDSLB	0.053
DSLB	0.053
COVEY*YEAR	0.021
SEASON	0.015
AGE*COVEY	0.015
SEASON*YEAR	0.011
SEX*COVEY	0.003

AGE*SEASON	0.001
SEX*SEASON	<0.001
AGE*SEX	<0.001

[a] See Table 1 for description of covariates.

Table 4. Odds ratios (95% CI) of daily survival rate for Northern Bobwhites by season of burn of most recent prescribed fire. Growing season fires are those conducted between 1 April and 1 September while dormant season fires are those between 2 September and 31 March. Unburned areas are those that have not been burned within the previous 10 years. An odds ratio describes the odds of daily survival for an individual in the *comparison state* contrasted with an individual in the *reference state*. The odds of survival are similar between states if the confidence interval encompasses 1.

	Comparison state		
Reference state	Growing season burn	Dormant season burn	Unburned
Growing season burn		0.663	0.727
		(0.500-0.879)	(0.504-1.047)
Dormant season burn	1.508		1.096
	(1.138-2.000)		(0.811-1.482)
Unburned	1.376	0.912	
	(0.955-1.983)	(0.675-1.234)	

Table 5. Odds ratios (95% CI) for daily survival rate for Northern Bobwhites by timber type. An odds ratio describes the odds of survival for an individual in the *comparison state* contrasted with an individual in the *reference state*. The odds of survival in both states are similar if the confidence interval encompasses 1.

	Comparison state				
Reference state	Pine	Pine-hardwood	Hardwood-upland	Hardwood-bottomland	Other (food plot, etc.)
Pine		0.587	0.972	0.495	0.864
		(0.412-0.837)	(0.669-1.413)	(0.325-0.754)	(0.693-1.077)
Pine-hardwood	1.704		1.657	0.844	1.472
	(1.195-2.429)		(1.003-2.737)	(0.599-1.190)	(1.073-2.021)
Hardwood-upland	1.028	0.604		0.510	0.889
	(0.708-1.494)	(0.365-0.997)		(0.296-0.876)	(0.583-1.354)
Hardwood-bottomland	2.018	1.185	1.962		1.744
	(1.326-3.072)	(0.840-1.670)	(1.141-3.375)		(1.161-2.621)
Other (food plot, etc.)	1.157	0.679	1.125	0.573	
	(0.928-1.442)	(0.459-0.932)	(0.739-1.714)	(0.381-0.862)	

Fig. 1. Group smoothed plots of continuous covariates used in analyses of daily survival rate of Northern Bobwhites at Conecuh National Forest, AL, 2002-2004. Dashed lines indicate the predicted linear effect between the continuous covariate and daily survival rate of bobwhites. The assumption of linearity in the logit appears supported for DIST (*a*), but ambiguous for DSLB (*b*) and GSDSLB (*c*).

Fig. 2. Change in daily survival rate (DSR) over range of mean minimum daily movement values (DIST) of Northern Bobwhites at Conecuh National Forest, AL, 2002-2004 and histogram of observed values of DIST. Values of DSR are computed from model averaged parameter estimates for the reference condition (i.e., DSR for subadult Bobwhites in the Unburned state and Other [food plot, etc.] timber type). Maximum observed DIST was 9874m, and 37 observations were > 2600m.

Fig. 3. Estimates of daily survival rate (DSR) of Northern Bobwhites at Conecuh National Forest, AL, 2002-2004 according to groupings by age, season of most recent prescribed fire (DSB =dormant season; GSB = growing season; UB = unburned), and timber type. Daily movement rate was also an important parameter in models of DSR of Northern Bobwhites. Survival values in this figure can be interpreted as those for an individual that moved 0 m day^{-1}; thus, values in this figure can be interpreted as intercept values in Figure 2.

Fig. 4. Group smoothed plots of continuous covariates used in analyses of daily movement rate (DMR) of Northern Bobwhites at Conecuh National Forest, AL, 2002-2004. Plot suggested a negative exponential relationship between DSLB and DMR (*a*). The plot for GSDSLB (*b*) suggests a linear relationship and the dashed line approximates this effect. DSLB was transformed accordingly and the solid lines represent the transformed function. See METHODS for transformation function for DSLB. The *a priori* model set for DMR include transformed values of DSLB while GSDSLB was included without transformation.

Fig. 5. Q-Q plots for each level of covariates in SIC best models of DMR: (*a*) whether an individual was in a food plot or not (FOOD) and (*b*) the interaction of season and calendar year of study (SEASON*YEAR). The group of data corresponding to a particular level of FOOD or SEASON*YEAR are appropriately described by the Weibull distribution if the pattern of points is linear.

Fig. 6. Mean DMR by SEASON*YEAR for Northern Bobwhites at Conecuh National Forest, AL, 2002-2004. SEASON describes the covey (2 October to 7 April), prenest (8 April to 21 May), nest (22 May to 1 September), and postnest (2 September to 1 October) periods. See METHODS for computation of mean values from a Weibull process (i.e., DMR).

Fig. 1*a*

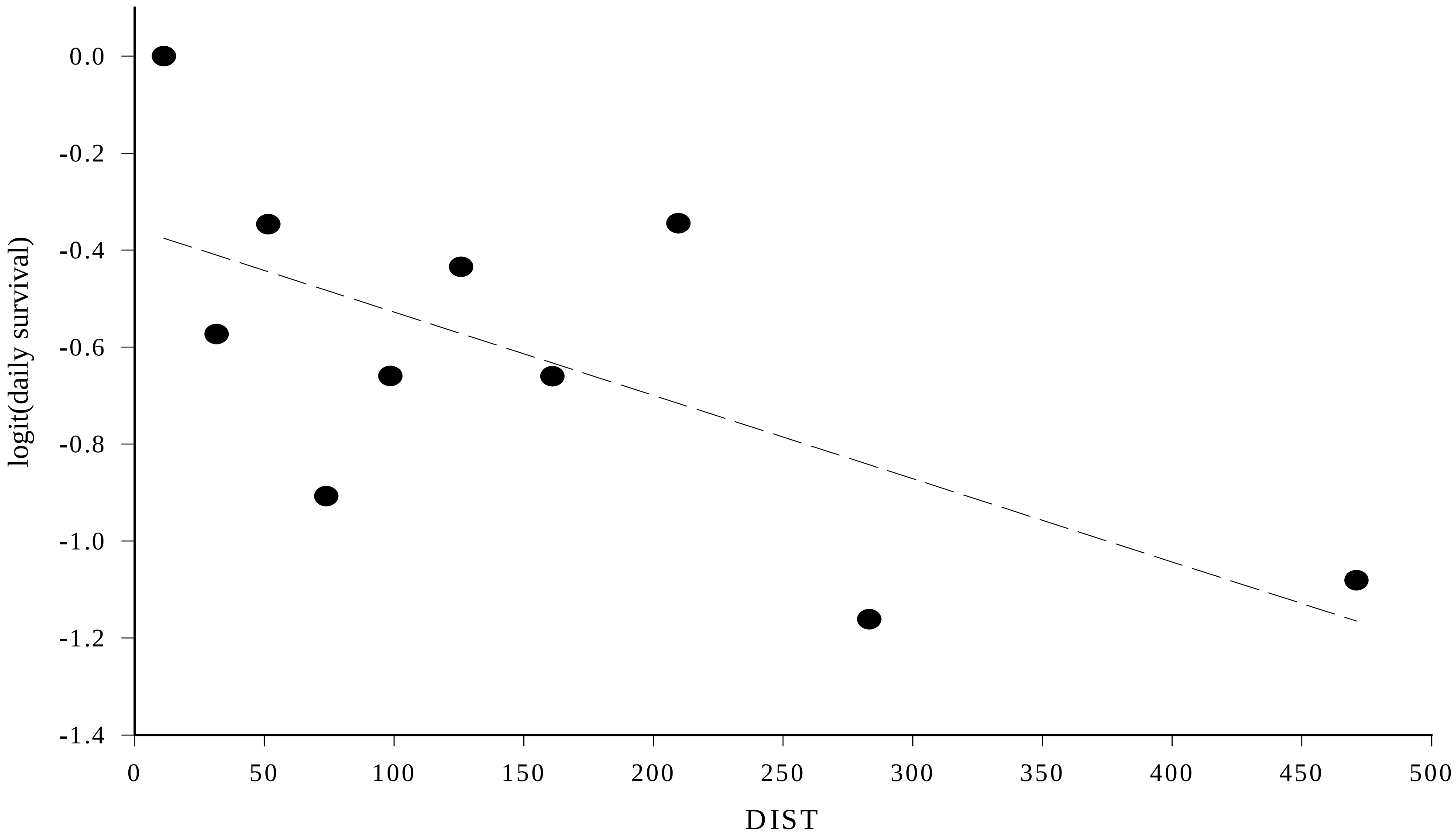
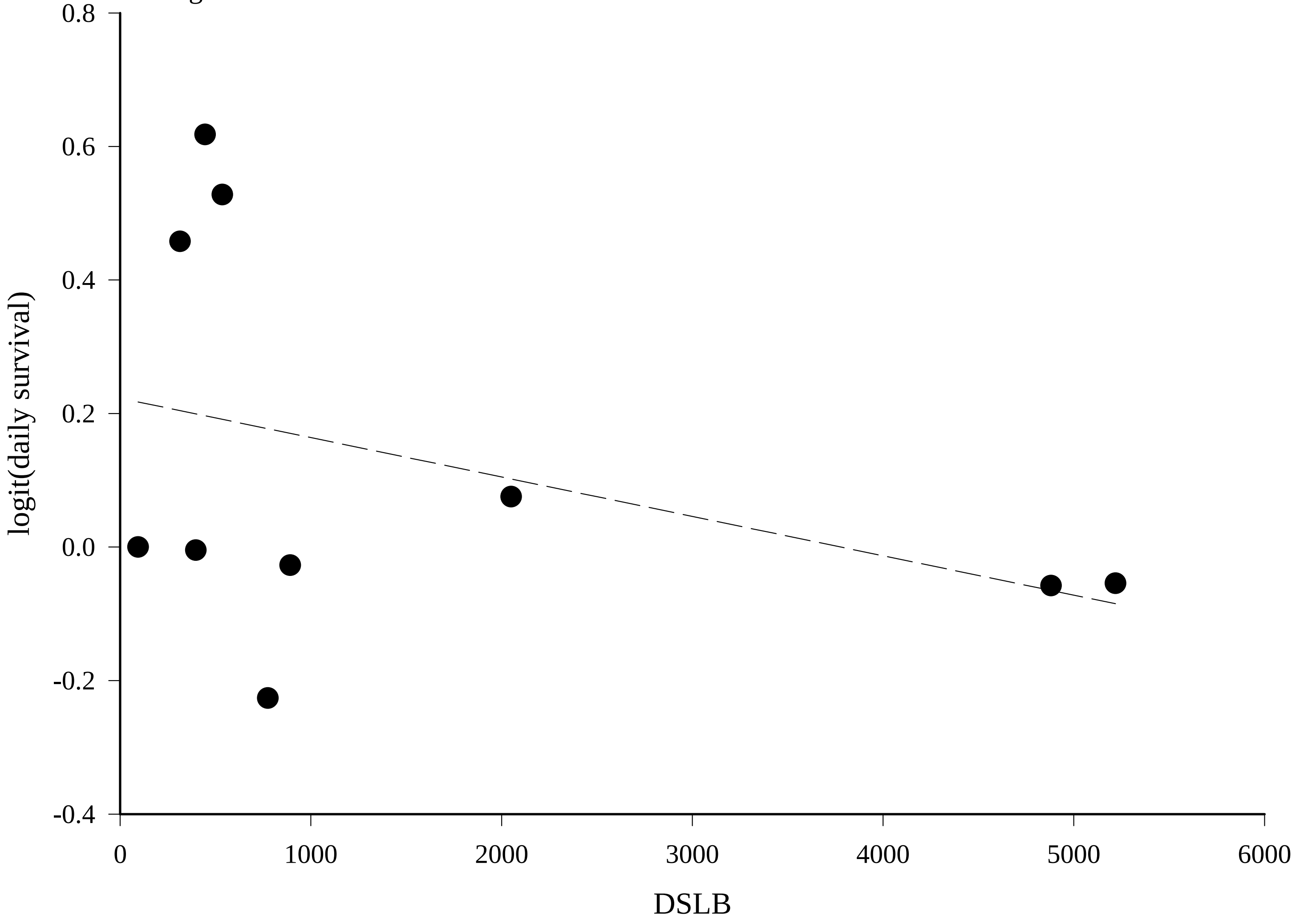

0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-1.2
-1.4
logit(daily survival)
0
50
100
150
200
250
300
350
400
450
500
DIST

Fig. 1*b*


0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
logit(daily survival)
0
1000
2000
3000
4000
5000
6000
DSLB

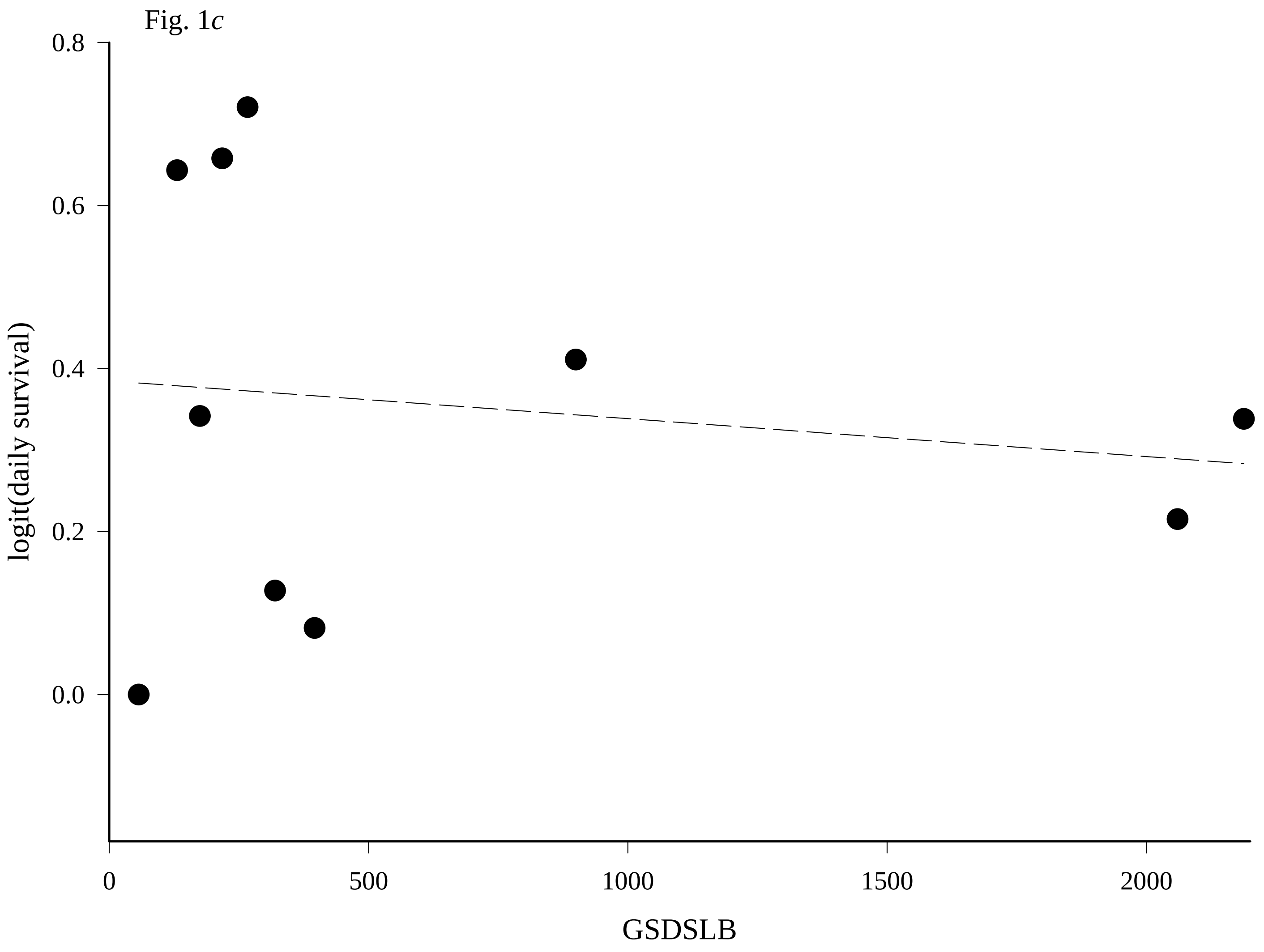


Fig. 1*c*
0.8
0.6
0.4
0.2
0.0
logit(daily survival)
0
500
1000
1500
2000
GSDSLB

Fig. 2

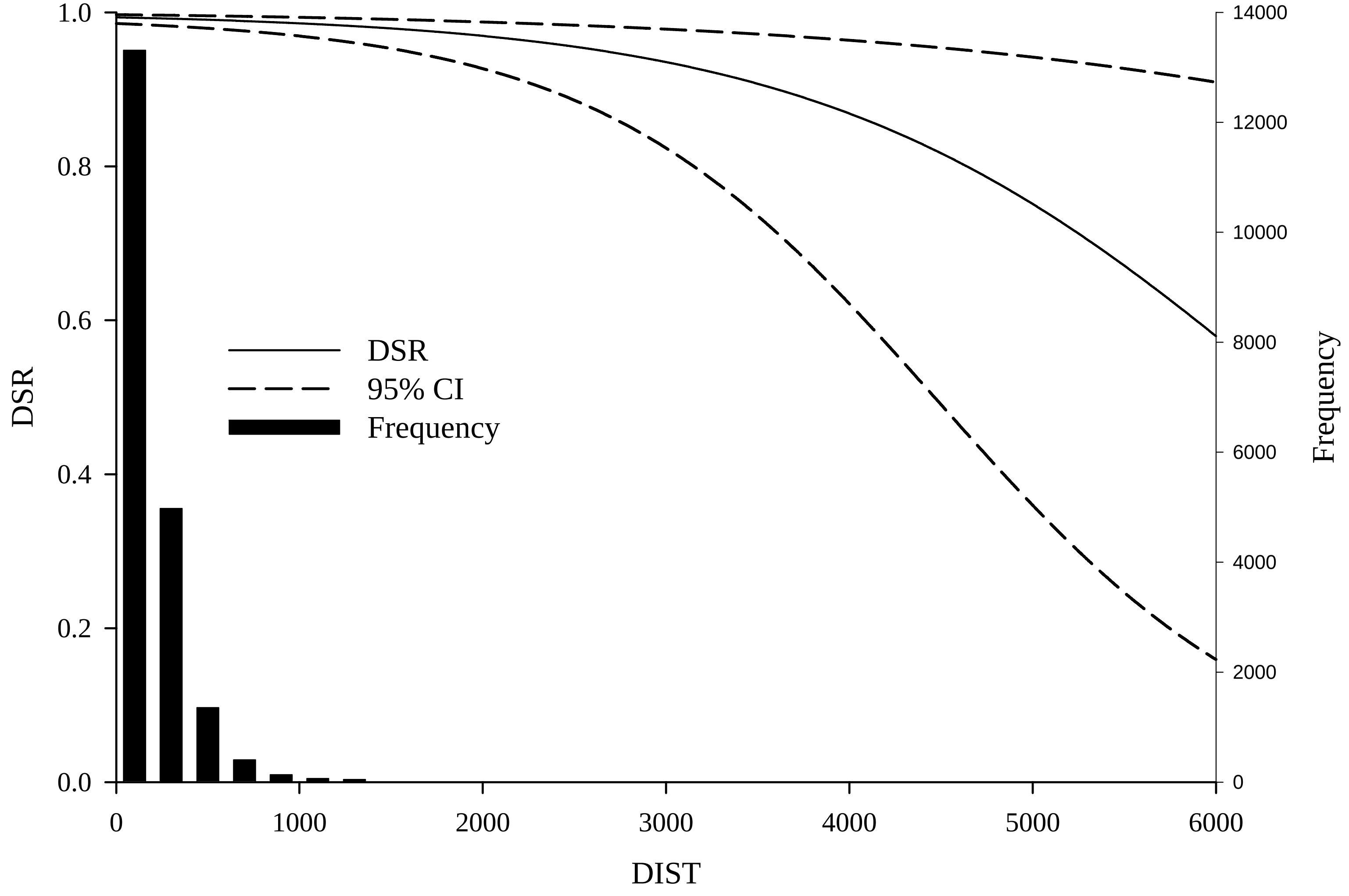

1.0
0.8
0.6
0.4
0.2
0.0
DSR
0
1000
2000
3000
4000
5000
6000
DIST
14000
12000
10000
8000
6000
4000
2000
0
Frequency
DSR
95% CI
Frequency

Fig. 3

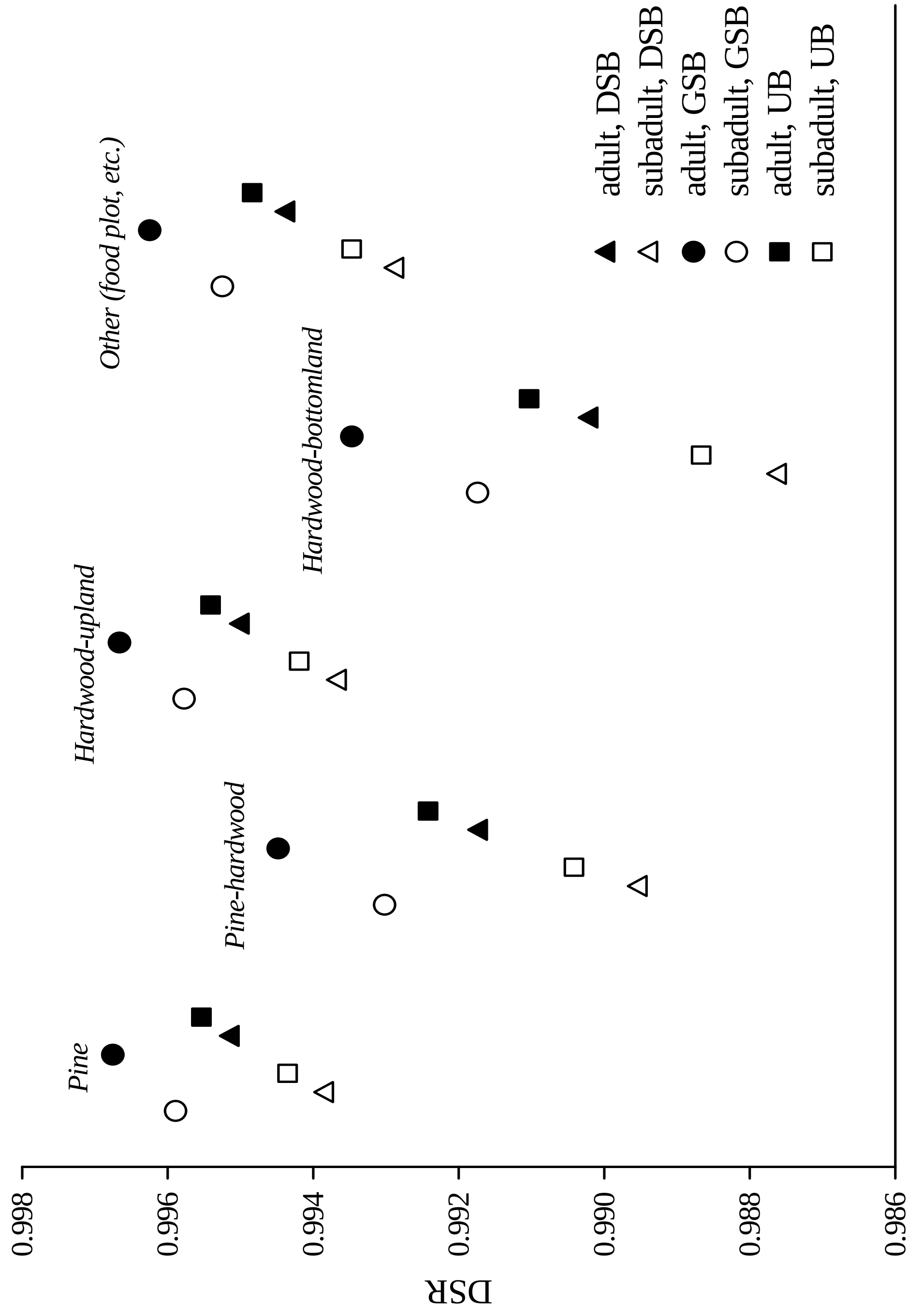

DSR
0.998
0.996
0.994
0.992
0.990
0.988
0.986
Pine
Pine-hardwood
Hardwood-upland
Hardwood-bottomland
Other (food plot, etc.)
▲ adult, DSB
△ subadult, DSB
● adult, GSB
○ subadult, GSB
■ adult, UB
□ subadult, UB

Fig. 4*a*

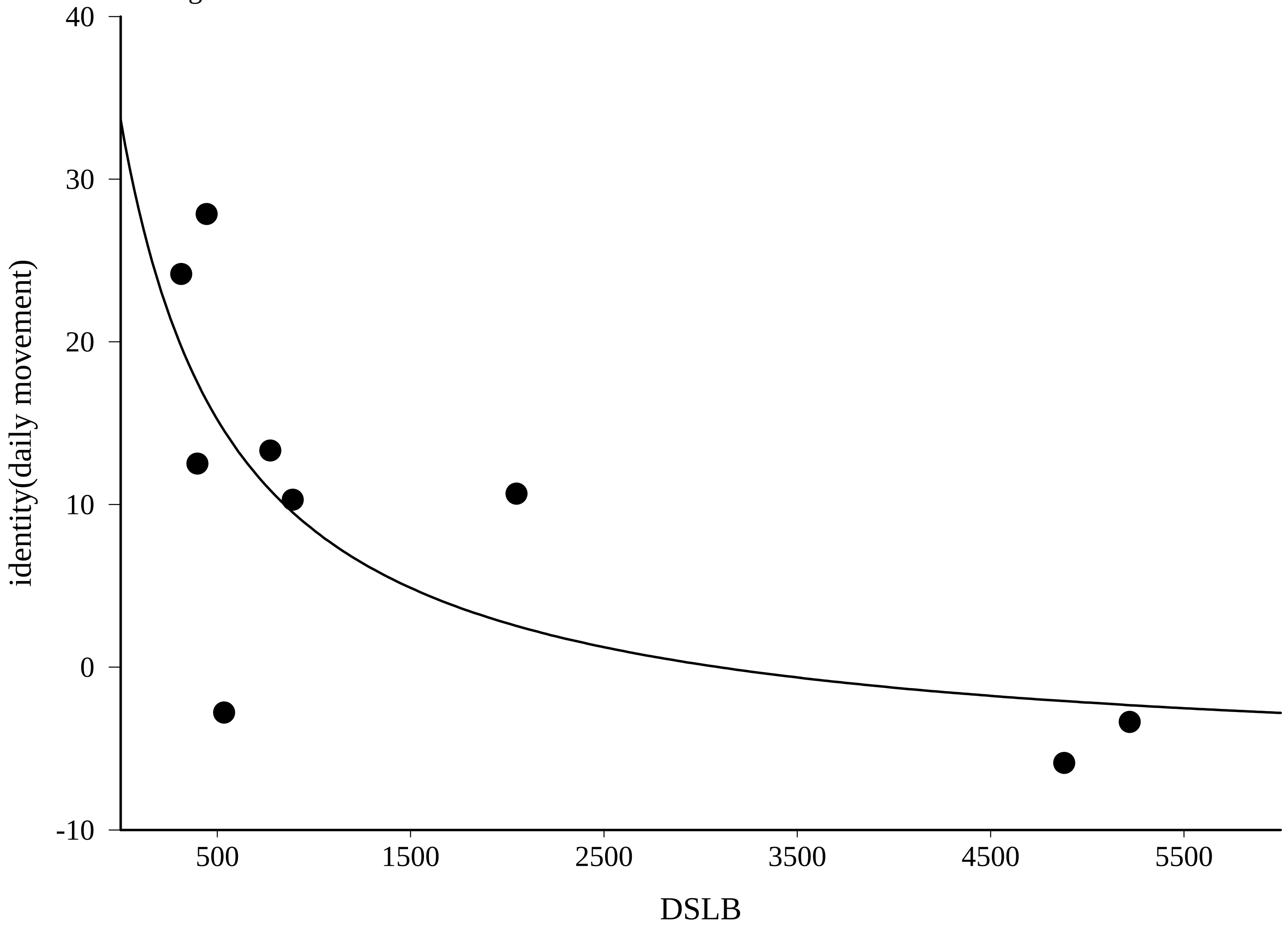

40
30
20
10
0
-10
identity(daily movement)
500
1500
2500
3500
4500
5500
DSLB

Fig. 4*b*

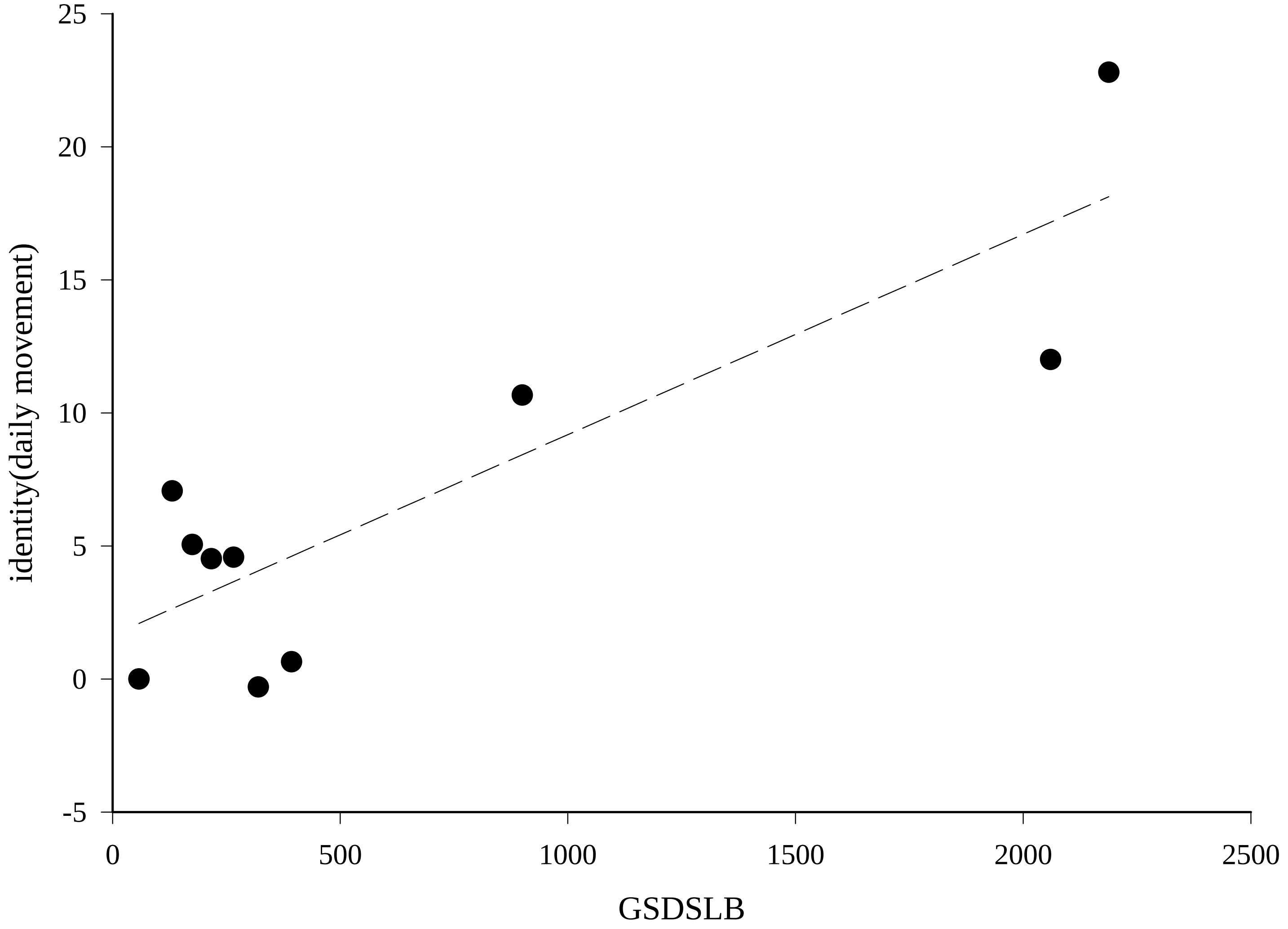

identity(daily movement)
25
20
15
10
5
0
-5
0
500
1000
1500
2000
2500
GSDSLB

Fig. 5*a*

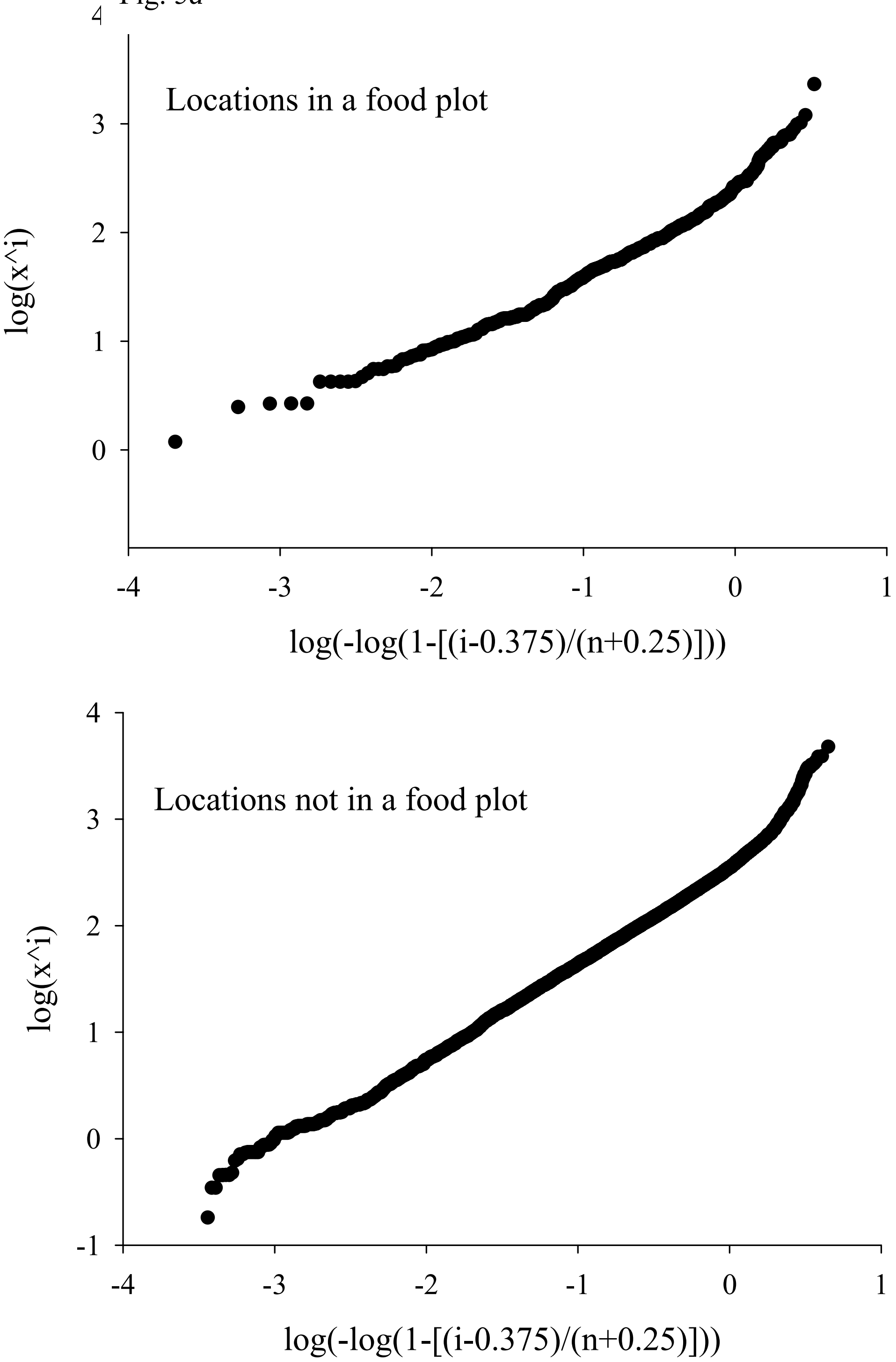

4
Locations in a food plot
3
2
1
0
log(x^i)
-4
-3
-2
-1
0
1
log(-log(1-[(i-0.375)/(n+0.25)]))
4
Locations not in a food plot
3
2
1
0
-1
log(x^i)
-4
-3
-2
-1
0
1
log(-log(1-[(i-0.375)/(n+0.25)]))

Fig. 5*b*

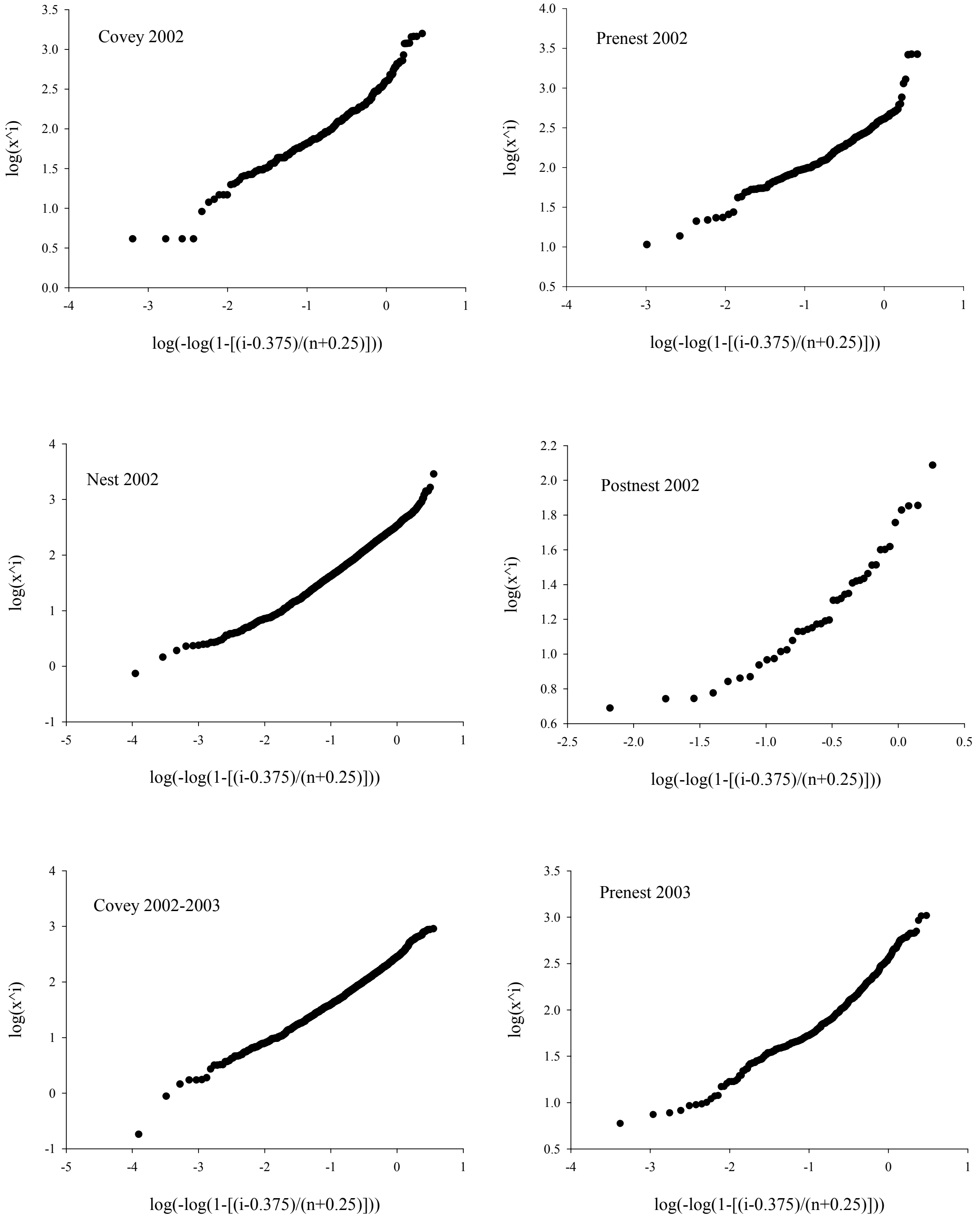

Covey 2002
Prenest 2002
Nest 2002
Postnest 2002
Covey 2002-2003
Prenest 2003
log(x^i)
log(-log(1-[(i-0.375)/(n+0.25)]))
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
0.6
0.8
1.2
1.4
1.6
1.8
2.2
-5
-4
-3
-2
-1
0
1
2
3
4
-2.5
-2.0
-1.5
-1.0
-0.5

Fig. 5*b*

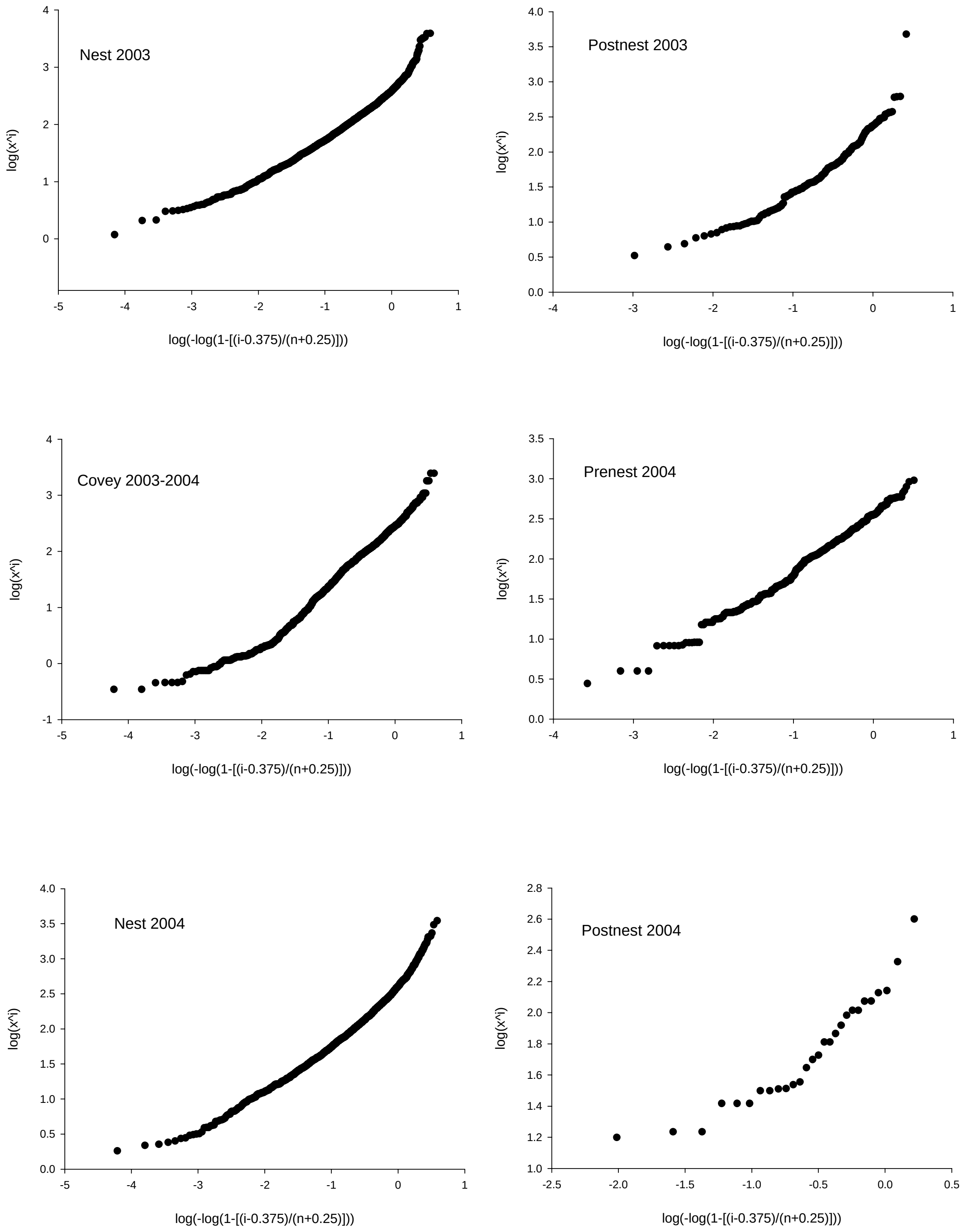
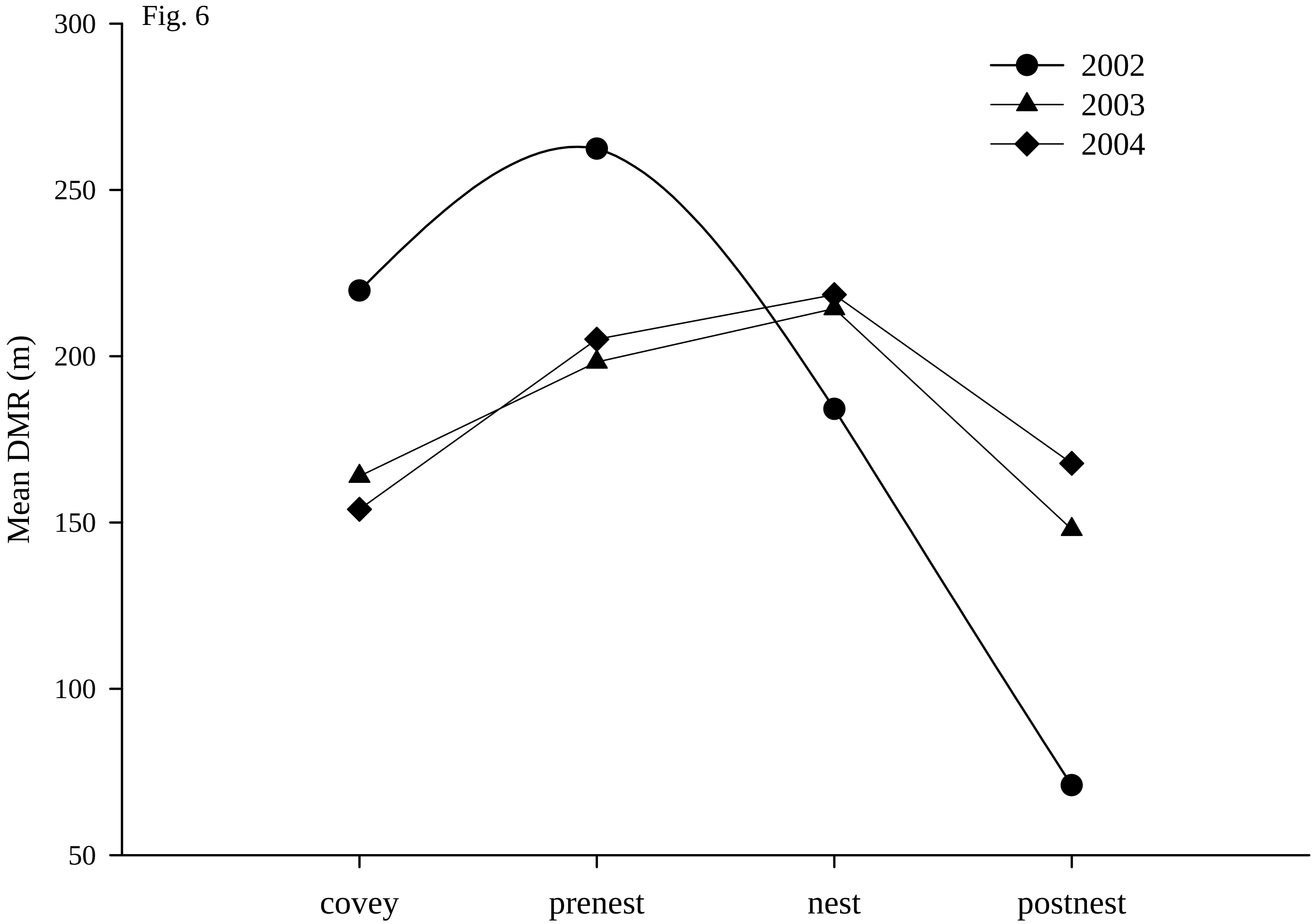

Nest 2003
log(x^i)
4
3
2
1
0
-5
-4
-3
-2
-1
0
1
log(-log(1-[(i-0.375)/(n+0.25)]))
Postnest 2003
log(x^i)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-4
-3
-2
-1
0
1
log(-log(1-[(i-0.375)/(n+0.25)]))
Covey 2003-2004
log(x^i)
4
3
2
1
0
-1
-5
-4
-3
-2
-1
0
1
log(-log(1-[(i-0.375)/(n+0.25)]))
Prenest 2004
log(x^i)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-4
-3
-2
-1
0
1
log(-log(1-[(i-0.375)/(n+0.25)]))
Nest 2004
log(x^i)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-5
-4
-3
-2
-1
0
1
log(-log(1-[(i-0.375)/(n+0.25)]))
Postnest 2004
log(x^i)
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5
log(-log(1-[(i-0.375)/(n+0.25)]))

Fig. 6


2002
2003
2004
300
250
200
150
100
50
Mean DMR (m)
covey
prenest
nest
postnest

IV. NORTHERN BOBWHITES IN A FIRE-MAINTAINED LONGLEAF PINE LANDSCAPE: MATRIX MODELS OF POPULATIONS IN DECLINE AND THE QUANTITATIVE RANKING OF REMEDIAL CONSERVATION ACTIONS

Abstract. Northern Bobwhites (*Colinus virginianus*) inhabit the fire-maintained longleaf pine ecosystem, and previous research has shown certain parts of Northern Bobwhite life history varies with respect to the season of year prescribed fire is used in this habitat type. Given that Northern Bobwhite populations are in decline throughout their geographic range and fire-maintained longleaf pine forests potentially represent quality habitat for Northern Bobwhites, examination of Northern Bobwhite population dynamics in longleaf pine forests managed with prescribed fire may guide remedial conservation actions for Northern Bobwhite populations. I developed 2-stage (i.e., subadult and adult) periodic matrix population models to describe population dynamics of Northern Bobwhites in longleaf pine forests managed with triennial prescribed fire during either the growing (i.e., 1 April to 1 September) or dormant (i.e., 2 September to 31 March) season. Within matrix population models representing longleaf pine forests managed with growing or dormant season prescribed fire, I quantitatively ranked hypothetical conservation scenarios with a calculus-based, multivariate perturbation technique. Increases in survival across both age-classes during the non-breeding periods has the greatest

potential influence on asymptotic population growth rate for Northern Bobwhite populations in longleaf pine forests managed with triennial prescribed fire in the growing and dormant seasons. Conservation efforts that focus exclusively on maintenance of nesting and brood rearing habitat may not realize increases in population growth rate if survival during the non-breeding periods declines. Effective conservation efforts should focus on demography of Northern Bobwhites throughout the annual cycle.

INTRODUCTION

Population declines in many avian species are attributable to a variety of factors including loss of habitat (Trani et al. 2001), increasing fragmentation of landscapes (Askins 2000), and degradation of habitat quality (Saab and Powell 2005). Among areas where diminished habitat quality is a concern, reduction in or the suppression of natural fire is increasingly cited as a major cause of habitat degradation, especially in early successional habitats throughout North America (Hunter et al. 2001, Saab and Powell 2005). Fire is a critical component to early successional habitats primarily because of its role in creating and maintaining vegetative structure (McPherson 1997, Platt 1999). Despite renewed interest in fire as an aspect of regional ecology that may influence avian populations; much of the pertinent research has focused on changes in avian communities (Saab and Powell 2005). While this research is laying the groundwork for greater understanding of the influence of fire on avian life histories, investigation of species specific demographic responses to fire is necessary for conservation actions to be maximally effective (e.g., Holmes et al. 1996).

Loss of the longleaf pine (*Pinus palustris*) ecosystem is one of the best case studies concerning the impact of anthropogenic fire suppression on avian species (Stoddard 1931, Askins 2000, Dickson 2002, Provencher et al. 2002, Engstrom et al. 2005, Tucker et al. 2006). Longleaf pine ecosystem harbors much faunal (Engstrom 1993, Folkerts et al. 1993, Guyer and Bailey 1993) and floral (Harcombe et al. 1993, Peet and Allard 1993) biodiversity; however, this diversity is only realized when fires, either natural lightning-ignited or anthropogenic prescribed fire, occur frequently (i.e., every 2-8 years; Frost 1998). Longer fire return intervals allow vegetative succession to reach conditions unsuitable for some avian species typical of the longleaf pine ecosystem (Tucker and Robinson 2003, Tucker et al. 2006).

Conservation of avian populations inhabiting this ecologically significant ecosystem depends on understanding the influence of fire on life histories. Further, placement of these life history effects into the context of the species' population dynamics will further increase efficacy of conservation efforts (e.g., Crowder et al. 1994). Northern Bobwhite (*Colinus virginianus*), a small gallinaceous bird distributed throughout eastern US and northeastern Mexico (Brennan 1999), is a common resident in fire-maintained longleaf pine forests (Engstrom et al. 2005). Range-wide fire suppression has led to substantial declines in populations within the longleaf pine ecosystem (Dimmick et al. 2002, Sauer et al. 2005). Given that there is renewed interest in restoration of longleaf pine forests (e.g., Kirkman et al. 2004), it is also important to understand how aspects of Northern Bobwhite life history and population dynamics respond to variation in prescribed fire regimes. Chapters II and III addressed the differences in productivity and seasonal survival of Northern Bobwhites in longleaf pine forests managed with triennial prescribed fire during either the growing (i.e., longleaf pine forests burned during 1 April to 1 September) or dormant (i.e., longleaf pine forests burned during 2 September to 31 March; Robbins and Myers 1992) season. These results will better aid remedial conservation actions for Northern Bobwhites in longleaf pine forests if they are placed within the context of Northern Bobwhite population dynamics.

The objectives of this paper are twofold. First, I investigate the demographic differences of Northern Bobwhites in longleaf pine forests managed with growing or dormant season prescribed fire, and the contribution of differences in demography to the difference in the expected asymptotic population growth rates (λ) in each burn type. Chapter III documented differences in daily survival rate by season of burn, where survival was higher in longleaf pine forests managed with growing season prescribed fire as compared to longleaf pine forests managed with dormant season prescribed fire. Longleaf pine forests managed with growing season prescribed fire tend to have a vegetative architecture (i.e., minimal midstory and abundant herbaceous and shrubby understory) more suitable to Northern Bobwhites. Longleaf pine forests managed with dormant season prescribed fire tend to have greater proportional of hardwoods in the midstory which shade out herbaceous plant species in the midstory (Waldrop et al. 1992).

The second objective was to quantitatively rank the effect on λ of various hypothetical conservation scenarios for Northern Bobwhites in longleaf pine forests managed with triennial prescribed fire either in the growing or dormant season. I discuss results in the context of Northern Bobwhite population ecology and development of effective conservation action for reversing the trend of Northern Bobwhite population declines.

METHODS

NORTHERN BOBWHITE PERIODIC MATRIX POPULATION MODEL CONSTRUCTION AND DEMOGRAPHIC ESTIMATES

I constructed periodic matrix models to reflect demography of Northern Bobwhites in each of four periods: breeding (1 June to 31 August), fall (1 September to 30 November), winter (1 December to 28 February), and spring (1 March to 31 May). Chapter III documented variation in daily survival rate, which was most associated with patterns in seasonal mobility. The periods identified in Chapter III were unequal in length, but because inference from perturbation analyses of lower level parameters (i.e., demographic parameters that combine to be expressed as a matrix element, e.g. nest success, which is a component of fertility) in periodic matrix models maybe obscured when period lengths are unequal (*T. H. Folk unpublished data*), I utilize periodic matrices to model periods of similar length. Period survival rates for use in periodic matrices are, however, composed of different daily survival rates described in Chapter III. I describe

Northern Bobwhite population dynamics with periodic matrix models that take the following form:

$$\mathbf{B_{FA}} = \begin{pmatrix} P_{FA(s)} & 0 \\ 0 & P_{FA(a)} \end{pmatrix}, \ \mathbf{B_{WI}} = \begin{pmatrix} P_{WI(s)} & 0 \\ 0 & P_{WI(a)} \end{pmatrix}, \mathbf{B_{SP}} = \begin{pmatrix} P_{SP(s)} & 0 \\ 0 & P_{SP(a)} \end{pmatrix},$$

$$\text{and } \mathbf{B_{BR}} = \begin{pmatrix} F_s & F_a \\ P_{BR(s)} & P_{BR(a)} \end{pmatrix}$$

where $\mathbf{B}_x$ represents the projection matrix associated with period *x* (i.e, *FA* = fall, *WI* = winter, *SP* = spring, and *BR* = breeding). Per projection matrix, survival over period *x* for age class *y* is described by $P_{x(y)}$ where subadults are described as $P_{x(s)}$ and adults as $P_{x(a)}$ (i.e., subadults hatched the previous breeding period and adults hatched > 1 breeding period prior). Fertility is expressed as F_y for age class *y*, and calculated as follows:

$$F_y = \omega_y * \delta_y * \phi_y * \gamma * \upsilon$$

where ω_y is nests female^{-1} period^{-1} of age class *y*, δ_y is clutch size nest^{-1} of age class *y*, ϕ_y nest success of age class *y*, γ age ratio at hatch, and υ is chick recruitment to a fall population. I conducted perturbation analyses of the above periodic matrix models; however, the effect of absolute (i.e., sensitivities) and proportional (i.e., elasticities) perturbations were estimated by implicit differentiation (i.e., $\partial\lambda/\partial a_{ij}$) of the characteristic equation of the annual matrix $\mathbf{A}$, where $\mathbf{A} = \mathbf{B_{FA}B_{WI}B_{SP}B_{NE}}$ and λ is the dominant eigenvalue of $\mathbf{A}$ (Lebreton 2005).

DEMOGRAPHIC ESTIMATES OF NORTHERN BOBWHITES

Chapter III documented substantial variation in Northern Bobwhite daily survival rate with respect to daily mobility and age of Northern Bobwhites (i.e., subadult or adult). Additionally, Northern Bobwhites in longleaf pine forests managed with growing season prescribed fire were 1.5 times more likely to survive a day than were Northern Bobwhites in longleaf pine forests managed with dormant season prescribed fire (Chapter III). Daily mobility of Northern Bobwhites, which had a substantial negative influence on daily survival rates, varied seasonally, but tended to be highest in the period prior to the breeding period (Chapter III). Thus, I generated daily survival rates for Northern Bobwhites according to age, season of burn of longleaf pine forests, and median estimates of daily mobility by periods as described in (Chapter III). The product of daily survival rates was used to compose period survival for matrix population models (Table 1).

I generated estimates of mean clutch size and nest success for a 24-day incubation period (Brennan 1999) from results of (Chapter II). I assume a 1:1 male: female sex ratio at hatch (Brennan 1999). Sample sizes of (Chapter II) were not large enough to produce a robust estimate of nests female^{-1} breeding period^{-1}; however, given Northern Bobwhite life history I assumed 2.5 nests female^{-1} breeding period^{-1}. Similar estimates have been given by Roseberry and Klimstra (1984). I lacked estimates of chick recruitment, but obtained an estimate of recruitment of chicks to a fall population from Szukaitis (2001). This study also was conducted recently (1999-2000) in the Southeastern Coastal Plain.

Although there is the potential for chick survival to vary between burn conditions and locations, several studies have failed to find consistent differences attributable to habitat type (Hammond 2001). Because I lacked demographic rates for a portion of the Northern Bobwhite life cycle, I do not discuss specific values of λ, but rather discuss comparative differences in demography between longleaf pine forests managed with either growing or dormant season prescribed fire.

LIFE TABLE RESPONSE EXPERIMENTS BETWEEN SEASONS OF BURN

I used life table response experiment (LTRE) for periodic matrix models (Chapter V) to evaluate the differences in bobwhite demography between longleaf pine forests managed with prescribed fire in either the growing or dormant seasons. LTREs compare the observed change in population growth rate between two or more matrix population models and decompose this difference into contribution values from individual demographic rates that simultaneously consider the sensitivities and observed changes of individual survival and fertility estimates. LTRE analyses of this type are referred to as a fixed, one-way design (Caswell 2001). Contribution values identify the change in demographics that contributed most to the difference in λ between the 2 conditions (Caswell 2001). I parameterized 2 separate periodic matrix models with demographic estimates for Northern Bobwhite that represent populations in longleaf pine forests managed with either growing or dormant season prescribed fire. In evaluating of demographic differences between burn types, I only considered differences in the matrix-level fertility value and did not consider differences in the lower-level values that composed fertility estimates (e.g., mean clutch size, nest success). I did this because in Chapter II I failed to find substantial differences in productivity due to season of burn.

QUANTITATIVE RANKING OF REMEDIAL CONSERVATION ACTIONS WITH DIRECTIONAL DERIVATIVES

While LTRE can be used to evaluate the effect of differences in demography among observed states, conservation measures developed from matrix population models are frequently based on prospective perturbation analysis of matrix models (Caswell 2001). Prospective perturbation analysis evaluates instantaneous change in λ in response to absolute (sensitivity) or proportional (elasticity) changes in demographic rates (Caswell 1978); typically, these calculations are conducted while assuming all other demographic rates are not perturbed. I developed a calculus-based, multivariate perturbation analysis that allows for evaluation of the sensitivity (or elasticity) of λ to perturbation of sets of demographic rates (Appendix). I defined the concept of multivariate perturbations for a matrix model as movement across a *demographic landscape* in proportion to a *hypothetical conservation scenario*, which is realized as a set of demographic perturbations. Hypothetical conservation scenarios may include simultaneous increases in demographic rates (e.g., increasing survival rates of all age classes in a particular period of the annual cycle) or simultaneous increases and decreases in demographic rates (e.g., density dependent processes that may depress one rate due to increases in another rate). Thus, a directional derivative is the rate of change (either positive or negative) in λ expected to result from a scenario. Directional derivatives may be positive or negative which represent increases or decreases, respectively, in λ for a hypothetical conservation scenario. For each scenario, the direction (positive or negative) of each perturbation must be defined. The evaluation of simultaneous demographic perturbations increases the biological reality and utility of perturbation analysis of matrix population models, and has a theoretical foundation from quantitative genetics and developmental evolutionary biology (Appendix).

I parameterized periodic matrix models for evaluation with directional derivatives similarly to those used for the above mentioned LTRE analysis (i.e., separate matrix models for Northern Bobwhites in longleaf pine forests managed with either growing or dormant season prescribed fire). In this perturbation analysis, however, I express fertility as composed of lower-level parameters. Directional derivatives for each conservation scenario were calculated and presented as absolute and proportional perturbations to demographic rates.

HYPOTHETICAL CONSERVATION SCENARIOS

I now describe rationale and development of hypothetical conservation scenarios for Northern Bobwhites in longleaf pine forests managed with triennial prescribed fire in either the growing or dormant season. My objective is to present scenarios that correspond to conservation scenarios as well as incorporate the effect of depressed survival rates as may result from lack of habitat management. Because the magnitude and sign of directional derivatives indicates the effect on λ, directional derivatives allow the quantitative ranking of remedial conservation scenarios and can be interpreted as the multivariate extension of traditional sensitivity and elasticity analyses (*sensu* Caswell 1978). Below, I describe the hypothetical conservation scenarios for Northern Bobwhite populations in longleaf pine forests managed with either triennial prescribed fire during the growing or dormant season. I compute 4 directional derivatives per scenario: a directional derivative per burn type (i.e., growing or dormant season burn) composed of either absolute (sensitivity) or proportional (elasticity) perturbations to demographic rates. Further, because conservation measures for Northern Bobwhites do not target specific age classes, I refer to perturbation of a demographic rate for both subadults and adults. Below are hypothetical conservation scenarios for Northern Bobwhites in longleaf pine forests managed with triennial prescribed fire.

1. *Perturbation with respect to the gradient vector*. Movement in the direction of the gradient vector represents perturbations that lead to the greatest potential influence on λ (i.e., maximization of the directional derivative). I compute the directional derivative in the direction of the gradient here because it establishes an upper bound for the effect of demographic perturbation on λ thus allowing for a better evaluation of hypothetical conservation scenarios.
2. *Increase in fertility*. Many conservation plans for Northern Bobwhites focus on the development and maintenance of habitat suitable for breeding activities (e.g., quality nest sites and chick rearing areas, etc.; Dimmick et al. 2002). Thus, I

evaluate the influence of increases in fertility measures during the breeding period only.

3. *Increase in survival during non-breeding periods.* Chapter V suggests that survival in the nonbreeding period may have a large influence on λ of Northern Bobwhites because of the importance for individuals to survive to their first breeding attempt. Thus, I evaluate increase in period survival rates in fall, winter, and spring (i.e., nonbreeding periods).
4. *Increase fertility and decrease survival during non-breeding periods*. Conservation strategies aimed towards increasing demographic rates in a single period may not lead to increases in λ if demographic rates in another period in the annual cycle are depressed. Pursuant to this point, I evaluate the influence that decreases in non-breeding period survival may have in conjunction with conservation measures directed towards increases in fertility.
5. *Increase survival during non-breeding periods and decrease fertility.* This scenario serves as a counterexample to scenario 4. This scenario will provide a better understanding of the influence of simultaneous increases and decreases in demographic rates on λ.
6. *Increase spring survival*. Chapter II documented an inverse relationship between daily survival rate and daily mobility rate of bobwhites in fire-maintained longleaf pine forests, and daily mobility was highest immediately prior to the breeding period. They suggested conservation measures may want to focus on habitat management to reduce mobility during this period.

7. *Increase fertility and spring survival*. I evaluate the combined effect of conservation efforts to increase fertility, pursuant to reasoning in scenario 2, and increase spring survival, pursuant to reasoning in scenario 6.
8. *Increase breeding period survival*. Northern Bobwhite life history is characterized by periodic increases in fertility. While a component of management is geared towards habitat management that capitalizes on increases in nest success, etc., I also wanted to evaluate the impact increased breeding period survival may have on λ.

RESULTS

Periodic matrix population models of Northern Bobwhite populations indicated populations were decreasing in longleaf pine forests managed with either growing (λ = 0.90) and dormant (λ = 0.63) season prescribed fire (Table 1). Breeding bird survey route level data for the area (Sauer et al. 2005) and independent point count data in longleaf pine forests managed with triennial prescribed fire (*D. Thurmond unpublished data; US Forest Service*) indicate similar trends. LTRE analysis indicated subadult survival in the spring period had the greatest positive contribution to differences in λ between burn types while adult fertility had a substantial negative contribution to differences in λ between burn types (Table 2). Contribution values for other demographic rates indicate observed variation between growing and dormant season managed longleaf pine habitats was minimal (Table 2).

Of all considered hypothetical conservation scenarios, increase in survival of both age classes in periods outside of the breeding period (i.e., fall, winter, and spring) had the largest potential influence on λ (Table 3). This result was consistent in both burn types and whether absolute or proportional perturbations to demographic rates were considered. Using the directional derivative as an upper bound to potential perturbation effects and considering proportional perturbations (i.e., elasticity), the directional derivative of this top ranked conservation scenario is 62.9% and 61.5% of the maximal potential effect on λ in growing and dormant season burned areas, respectively. Increases in fertility and survival during the spring period had the second largest potential positive impact on λ. Conservation scenarios that increased fertility and simultaneously decreased survival during periods outside of the breeding period have a potentially negative influence on λ. Other conservation scenarios were intermediate in their potential influence on λ (Table 3).

DISCUSSION

Remedial conservation actions for declining avian populations are a central focus for reversing population trends of many avian species in the longleaf pine ecosystem (Hunter et al. 1994, Askins 2000, Engstrom et al. 2005, Tucker et al. 2006). While numerous issues can influence population decline of a species (e.g., landscape fragmentation, habitat degradation, etc.), quantifying the influence of changes in demography, whether due to differences in habitats or time of year, etc., on population dynamics is an important component to ensuring the efficacy of conservation efforts. I approached the topic of declining Northern Bobwhite population in longleaf pine forests with use of periodic matrix population models in 2 types of perturbation analyses. First, retrospective analyses, like LTRE, provide an understanding of how observed variation in demography translates into variation in λ, but their utility in development of conservation measures is questionable (Caswell 2000). Second, conservation actions based on prospective perturbation analyses (i.e., sensitivity and elasticity) of matrix population models has increased the efficacy of conservation efforts (e.g., Crowder et al. 1994). However, the assumption behind these calculations that all rates, except the one of interest, are held constant is not biologically plausible. Further, there is no notion of a maximal influence on λ. The calculus-based, multivariate perturbation technique in the Appendix overcomes both of these limitations. Thus the analysis presented here provides a means of quantitative comparison of remedial conservation actions that affect more than one vital rate.

Directional derivatives suggest that increases in survival in the non-breeding periods (i.e., fall, winter, spring) can have the greatest potential influence on λ (Table 2), and account for the majority of the potential maximum influence of demographic rates on λ. This result appears robust due to the consistency of its top ranking whether perturbations to demographic rates are evaluated as absolute (i.e., gradient vector as composed of sensitivities) or proportional changes (i.e., gradient vector as composed of elasticities) and across both burn types (Table 3). LTRE between growing and dormant season managed longleaf pine stands also suggest that survival in non-breeding periods also influence differences in λ (Table 2). Differences in subadult survival just prior to the breeding period made the largest contribution to differences in λ between growing and dormant season burned longleaf pine forests (Table 2). Taken collectively, these results suggest that conservation actions aimed towards increasing survival for Northern Bobwhites between breeding periods will have the greatest potential influence on λ

Evaluation of directional derivates of the conservation scenario that included simultaneous increases and decreases in demographic rates reveal a potentially important dynamic of Northern Bobwhite population dynamics. Conservation measures for Northern Bobwhites typically center on the development and maintenance of habitat suitable for nesting and brood-rearing Northern Bobwhites (Dimmick et al. 2002). While increases in fertility during the breeding period will have a positive effect on λ, a simultaneous reduction in survival in the periods other than the breeding period can have a mitigating influence on population gains of increased fertility such that λ is not increased. This suggests results of conservation efforts focused exclusively on demographic rates in the breeding period may be negligible if survival between breeding periods declines. Conservation actions that ensure high survival during the nonbreeding periods will allow conservation efforts geared towards increasing fertility to be maximally effective.

Chapter II documented an inverse relationship between daily survival rate and daily movement rate. In turn, daily movement rate increased immediately prior to the breeding period. This suggested that development of habitats and landscapes that minimized movement would lead to increased survival rates. LTRE analysis indicates that subadult survival during the spring period had the largest contribution to variation in λ between growing and dormant season burned longleaf pine forests. However, when evaluating the potential influence of increasing spring period survival on λ, via decreasing movement rates, it has little influence as compared to other conservation scenarios and is less than half of the largest potential effect described by perturbation according to the gradient vector. Even so, there maybe benefit to increased movement prior to the breeding period if dispersal of Northern Bobwhites may allow for re-establishment of local populations that have been extirpated (Hanski 1999, Parvinen 2004). Future work should attempt to understand the importance of temporal and spatial variation in movement of Northern Bobwhites as this may be a viable alternative to restoring Northern Bobwhite populations.

It is important to note that development of periodic matrix models as done here does not include the probability of Northern Bobwhite movement between areas of differing burn types. Namely, the mathematics implemented here assumes that Northern Bobwhite movement among longleaf forests of both burn types is either negligible or equivalent. In fact, Chapter II documented substantial daily movement in this Northern Bobwhite population, although those analyses did not investigate asymmetrical movement between longleaf pine stands of differing burn history. Further investigation into asymmetrical movement could provide support for parameterization of matrix population models here or could lead to refinement of these periodic matrix models (Hunter and Caswell 2005) and analyses using directional derivatives.

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Table 1. Demographic estimates used in periodic matrix models of Northern Bobwhites in growing (i.e., 1 April to 1 September) or dormant (i.e., 2 September to 31 March) season burned longleaf pine forests. Demographic estimates are taken from Chapter II and III, and unpublished data. I obtained recruitment of chicks into the fall population from (i.e., 0.466) from Szukaitis (2001), and I assumed a 1:1 male:female sex ratio at hatch (Brennan 1999).

Dormant season	Fall period survival[1]	Winter period survival	Spring period survival	Breeding period survival	Nest success[2]	Mean clutch size
subadult	0.531	0.534	0.527	0.525	0.530	12.1
adult	0.578	0.581	0.574	0.573	0.356	12.1
Growing season						
subadult	0.612	0.615	0.608	0.607	0.512	11.4
adult	0.654	0.657	0.651	0.650	0.336	11.4

[1] Fall: 1 September to 30 November; Winter: 1 December to 28 February; Spring: 1 March to 31 May; Breeding period: 1 June to 31 August.

[2] Nest success for a 23-day incubation period.

Table 2. Contribution values that describe the most influential changes in demography between longleaf pine forests managed with either growing (i.e., 1 April to 1 September) or dormant (i.e., 2 September to 31 March) season prescribed fire.

	Period			
Demographic rate	Breeding[1]	Fall	Winter	Spring
subadult survival	0.042	0.038	0.038	0.258
adult survival	0.009	0.009	0.009	0.054
subadult fertility	-0.139	-	-	-
adult fertility	-0.260	-	-	-

[1] Fall: 1 September to 30 November; Winter: 1 December to 28 February; Spring: 1 March to 31 May; Breeding period: 1 June to 31 August.

Table 3. Quantitative ranking of remedial conservation scenarios for Northern Bobwhite populations in longleaf pine forests managed with prescribed fire during the growing (i.e., 1 April to 1 September) or dormant (i.e., 2 September to 31 March) season. Quantities presented are the value of the directional derivative (i.e., $D_{\mathbf{u}}\lambda_1$) for perturbations corresponding to conservation scenarios. Directional derivative values were computed as absolute (i.e., $\partial\lambda_1/\partial a_{ij}$) and proportional (i.e., $\left[\left(a_{ij}/\lambda_1\right)\left(\partial\lambda_1/\partial a_{ij}\right)\right]$) perturbations to demographic rate a_{ij}. The gradient scenario represents perturbations of all a_{ij} and quantifies the maximum potential effect on λ_1. Conservation scenarios are assumed to influence both age classes (e.g., increase spring survival would apply to subadults [$P_{SP(s)}$] and adults [$P_{SP(a)}$] equally).

	Dormant season prescribed fire		*Growing season prescribed fire*	
Conservation scenario	$D_{\mathbf{u}}\lambda_1\left(\partial\lambda_1/\partial a_{ij}\right)$	$D_{\mathbf{u}}\lambda_1\left[\left(a_{ij}/\lambda_1\right)\left(\partial\lambda_1/\partial a_{ij}\right)\right]$	$D_{\mathbf{u}}\lambda_1\left(\partial\lambda_1/\partial a_{ij}\right)$	$D_{\mathbf{u}}\lambda_1\left[\left(a_{ij}/\lambda_1\right)\left(\partial\lambda_1/\partial a_{ij}\right)\right]$
Gradient	2.016	1.852	2.578	1.814
Increase fall, winter, and spring period survival[1]	1.335	1.139	1.661	1.141
Increase spring period survival, increase fertility	1.054	1.107	1.426	1.097
Increase spring period survival	0.776	0.658	0.964	0.659
Increase fertility	0.742	0.891	1.065	0.877
Increase breeding period survival	0.104	0.088	0.150	0.103

Increase fall, winter, and spring period survival, and decrease fertility	0.564	0.319	0.613	0.329
Increase fertility, decrease fall, winter, and spring period survival	-0.564	-0.319	-0.613	-0.329

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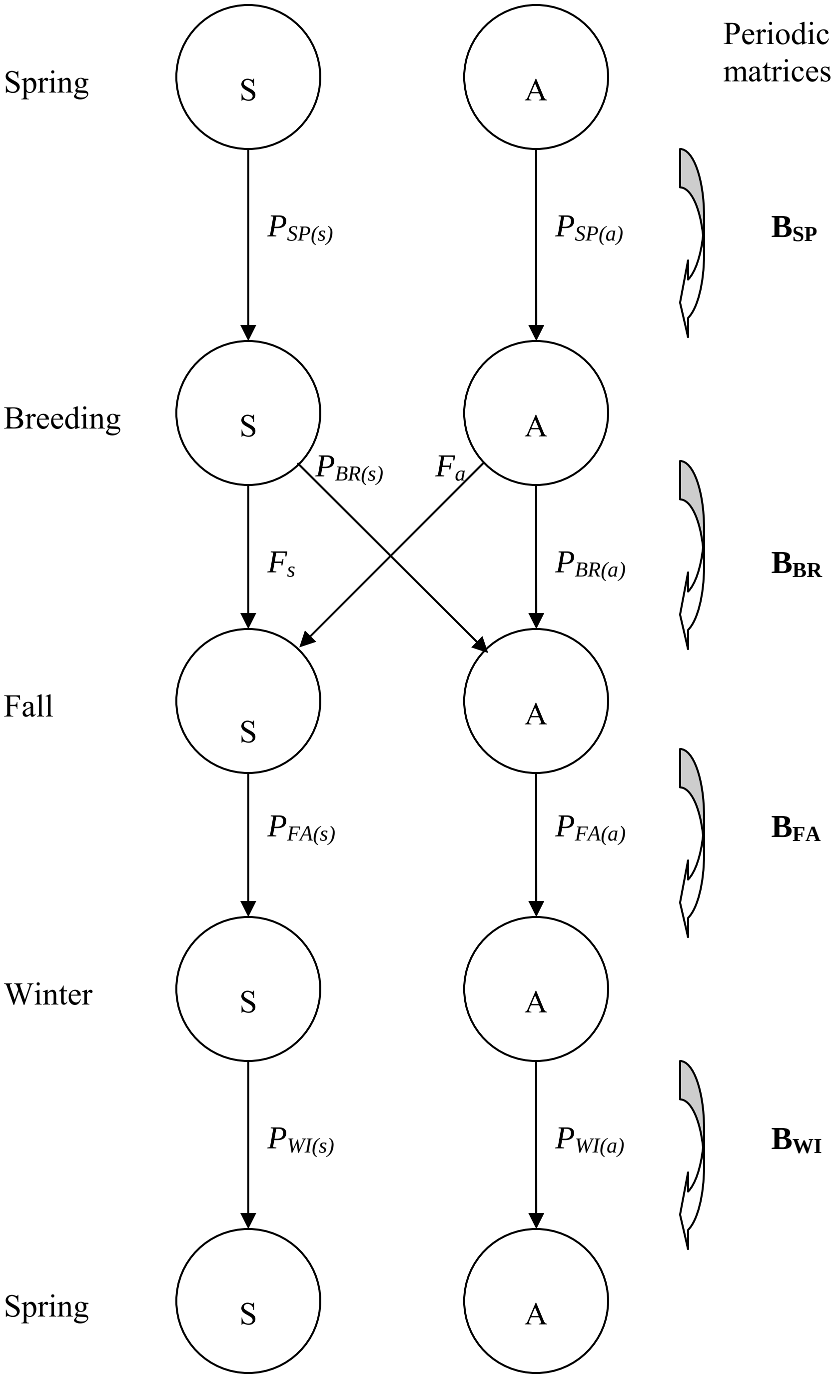
[1] Fall: 1 September to 30 November; Winter: 1 December to 28 February; Spring: 1 March to 31 May; Breeding period: 1 June to 31 August.

FIGURE 1. Seasonal life cycle graph for Northern Bobwhites in longleaf pine forests. Each circle represents subadults (i.e., S) or adults (i.e., A) across the fall (1 September to 30 November), winter (1 December to 28 February), spring (1 March to 31 May), and breeding (1 June to 31 August) periods. Period survival rates are given as $P_{x(y)}$ where x is the fall (FA), winter (WI), spring (SP), and breeding (BR) periods for age class y (s = subadults, a = adults). Fertility of subadults and adults is given as F_s and F_a, respectively.


Periodic matrices
Spring
S
A
$P_{SP(s)}$
$P_{SP(a)}$
$\mathbf{B_{SP}}$
Breeding
S
A
$P_{BR(s)}$
F_a
F_s
$P_{BR(a)}$
$\mathbf{B_{BR}}$
Fall
S
A
$P_{FA(s)}$
$P_{FA(a)}$
$\mathbf{B_{FA}}$
Winter
S
A
$P_{WI(s)}$
$P_{WI(a)}$
$\mathbf{B_{WI}}$
Spring
S
A

V. VARIATION IN NORTHERN BOBWHITE DEMOGRAPHY ALONG TWO TEMPORAL SCALES

Abstract. Quantification and understanding of demographic variation across intra- and inter-annual temporal scales can benefit development of theoretical models of evolution and applied conservation of the species. I used long-term survey data for northern bobwhites (*Colinus virginianus*) collected at the northern and southern extent of its geographic range to develop matrix population models which would allow investigation of intra- and inter-annual patterns in bobwhite population dynamics. I first evaluated intra-annual patterns in the importance of a seasonal demographic rate to asymptotic population growth rate with prospective perturbation analysis (elasticity analysis). I then conducted retrospective analysis (life table response experiments) of inter-annual patterns in the contribution of observed changes in demography to the observed change in population growth rate. For intra-annual analyses, I predicted, based on life history theory, fertility in the earliest age class would have the greatest potential influence on asymptotic population growth rate. Instead, I found survival in the earliest age class during the nonbreeding season had the greatest potential influence in both the northern and southern populations. Examination of inter-annual variation in demography indicated variation in nonbreeding season survival in the earliest age class contributed the

most to observed changes in population growth rate in the northern population. In contrast, changes in fertility in the earliest age class in the southern population had the greatest influence on changes in population growth rate. Prospective elasticity analyses highlight the similarities in bobwhite demography throughout different parts of its geographic range, while retrospective life table response experiments revealed important patterns in the temporal differences of bobwhite life history at the northern and southern extent of its geographic range. Incorporating intra- and inter-annual changes in demographic rates into population models can provide a greater insight into a species' life history and population dynamics.

Introduction

Understanding the patterns and sources of demographic variability has long been a central focus of ecology (Kingsland 1985). This goal has been both practical, as in the case of improved management capabilities for a species (e.g., Senar et al. 2002, Lima et al. 2003), as well as hypothetical, represented by theoretical advances in areas such as population and evolutionary ecology (Tuljapurkar 1990, Hanski 1999, Roff 2002). The dynamic properties of populations have primarily been classified as either spatial or temporal in nature (Rhodes et al. 1996). Numerous theoretical advances have been made in understanding the potential importance of both spatial and temporal sources of demographic variability to overall population growth and viability (Pulliam 1988, Tuljapurkar 1990, Hanski 1999); however empirical investigations are needed to understand the applicability of these demographic theories to a range of life histories.

Temporal sources of demographic variability can either be assessed at the intra- or inter-annual time scales with variation along each temporal scale revealing important attributes of a species' life history. For example, examination of intra-annual variation within a life history can indicate portions of the annual cycle where conservation actions might be most effective (Lima et al. 2003). Inter-annual variability of seasonal rates can reveal levels of demographic stochasticity that operate within a population (Lande et al. 2003). Understanding how demography of a species varies with respect to temporal criteria will allow for a better understanding of life history theory (Horvitz and Schmeske 1995, Pfister 1998) and increase efficacy of conservation efforts (Lima et al. 2003).

I sought to evaluate intra- and inter-annual patterns in demography in a common North American galliform bird, northern bobwhite. Northern bobwhites are a small (178 g, Dunning 1993) bird inhabiting open habitats dominated by herbaceous/shrubby vegetation in the eastern United States (Brennan 1999). While bobwhites are one of the most extensively studied avian species (Scott 1985), populations have been declining throughout most of their range for ≥ 4 decades (Brennan 1999). Despite extensive estimation of survival and fertility rates (Brennan 1999), little work has sought to investigate patterns of demographic variability and how this influences population dynamics. In order to address intra- and inter-annual differences in demography, our strategy was to construct a matrix population model (Caswell 2001) to represent seasonal variations (i.e., breeding [2 April-15 November] and nonbreeding [16 November-1 April] season) in population dynamics for a bobwhite population in the northern (Wisconsin) and southern (Alabama) extent of its geographic range.

Life history theory predicts that the asymptotic population growth rate (λ_a , long-term growth rate of a population assuming demographic stability) of a species with low annual survival and high levels of fertility (i.e., number of females in age class *i*, at time *t+1*, per female in age class *i* at time *t*; Caswell 2001) should be influenced most by perturbations to fertility, especially in the younger age classes (Heppell et al. 2000, Sæther and Bakke 2000). Bobwhites are aptly described by this type of demographic structure (Brennan 1999, Chapter IV), and I predicted that changes in subadult (i.e., females that were less than one year old) fertility would most influence λ_a in both the northern and southern populations. This prediction was motivated because bobwhites have short generation time (Speake 1967), and reproduction should be an important component to long-term population persistence (Sæther and Bakke 2000); however, development of this life history construct (i.e., the "slow-fast" continuum) has primarily been assessed at an annual time scale (Heppell et al. 2000, Sæther and Bakke 2000). Recent advancements in life history theory suggest that demographic rates that contribute substantially to changes in population growth rate should be buffered against environmental variation (Pfister 1998; but see Morris and Doak 2004). Thus, I expected demographic rates with greater potential influence on population growth rate (i.e., higher elasticity values) to contribute less to observed change in population growth rate.

Materials and methods

I used survey data from northern bobwhite populations in Prairie Du Sac, Wisconsin (Kabat and Thompson 1963; 43.29°N, 89.73°W) and Camp Hill, Alabama (Speake 1967; 32.80°N, 85.66°W) to estimate demographic rates for seasonally periodic (hereafter periodic) matrix population models of both populations. These datasets were chosen because of the duration of study (i.e., 10 years in Wisconsin and 13 years in Alabama), field methodologies were similar, and they represented northern (Wisconsin) and southern (Alabama) extent of the geographic range for bobwhites.

In Alabama, bobwhite populations were surveyed twice annually during 2-3 week intervals centered on or about 1 April and 15 November between 1951 and 1963 (Speake 1967). Bobwhite coveys were located repeatedly during the survey period with trained bird dogs and number of flushed birds were counted. This technique has been used reliably in other studies (e.g., Hudson et al. 1992). Bobwhite coveys located with bird dogs were revisited during the survey interval until counts of individuals stabilized (typically 3-4 encounters; Speake 1967). Speake (1967) provided supportive evidence that surveying bobwhites with trained bird dogs and covey counts accurately estimated total population size. During spring 1962, extensive live trapping was conducted in which 110 individuals were trapped and an additional 10 "trap shy" bobwhites were identified. Population estimates from the bird dog/covey count technique had estimated 119 individuals on the study site (Speake 1967). Bobwhites in Wisconsin were live trapped during the spring (early April) and fall (mid November) of 1942-1951 (Kabat and

Thompson 1963). This Wisconsin population was researched extensively by Errington (1945), and has been referred to frequently in the literature (Andrewartha and Birch 1954, Lack 1954, Fretwell 1972, Newton 1998).

Both Kabat and Thompson (1963) in Wisconsin and Speake (1967) in Alabama estimated total population size for the April and November survey periods. They also estimated abundance in November surveys by age class (i.e., subadult and adult). Bobwhite reproduction occurs primarily during the summer months of June through August (Brennan 1999). Therefore, subadults in the November survey hatched the preceding breeding season, while adults hatched at least 2 breeding seasons prior to the November census. Fall abundance estimates of subadults and adults in Wisconsin were determined directly through trapping data (Kabat and Thompson 1963), while in Alabama age ratios of surveyed birds were determined indirectly by multiplying the survey's fall abundance estimate by an age distribution determined annually from local and state hunter surveys (Speake 1967).

For periodic matrix construction, estimates of breeding and nonbreeding season survival and fertility were calculated from survey data. Breeding season survival estimates for subadults, P_{Bs}, and adults, P_{Ba}, were calculated as the proportional change in number of individuals present 1 April in year *t* and the number of adult bobwhites on 15 November in year *t*. Nonbreeding season survival estimates for subadults, P_{NBs}, and adults, P_{NBa}, were calculated as the proportional change in individuals between 15 November in year *t* and 1 April in year *t+1*. Subadult bobwhites mature to the adult age class just prior to the November survey (Brennan 1999). Because individual-based estimates of fertility were not available for either study site during the time frame of the respective studies, I used the anonymous reproduction technique to estimate fertility (Caswell 2001:173). Fertility (F_s and F_a for subadults and adults, respectively) was estimated as number of subadult females present at the 15 November survey per female counted on the 1 April survey. Periodic matrices were constructed to reflect the nonbreeding and breeding season and took the form:

$$\mathbf{B_{NB}} = \begin{pmatrix} P_{NBs} & 0 \\ 0 & P_{NBa} \end{pmatrix} \text{ and } \mathbf{B_B} = \begin{pmatrix} F_s & F_a \\ P_{Bs} & P_{Ba} \end{pmatrix},$$

where $\mathbf{B_{NB}}$ and $\mathbf{B_B}$ represent the projection matrices associated with the nonbreeding and breeding seasons, respectively. Thus, the annual matrix model is formed by

$$\mathbf{A} = \mathbf{B_{NB}} \mathbf{B_B} .$$

The life cycle can similarly be represented in a seasonal construct (Fig. 1).

I assumed that demographic rates did not differ between subadults and adults. This constraint was imposed by structure of the data (i.e., Kabat and Thompson 1963, Speake 1967); however, several studies have not found significant differences in either annual or seasonal survival due to age of bobwhites (Curtis et al. 1988, Pollock et al. 1989, Burger et al. 1995, Townsend et al. 2003). Although our assumption, justified by empirical evidence, is that demographic rates do not differ between ages, age structure, even in this simplistic model, is important for evaluation and interpretation of the life cycle. Estimation of demographic rates as done here assumes that no ingress or egress of individuals to the study population occurred. I feel this assumption is appropriate because the study areas were large (Wisconsin = 1820 ha, Alabama = 570 ha) in comparison to the size of a bobwhite's annual home range, and demographic rate estimates in this study were similar to other published demographic rate estimates of radio-marked individuals (Brennan 1999). I also used randomization tests to examine the difference in population growth rates of the Wisconsin and Alabama populations (Caswell 2001). Randomization tests returned the probability that 2 growth rates were different (i.e., $P[\lambda_{\text{Wisconsin}} = \lambda_{\text{Alabama}}]$). Confidence intervals for λ_a rate were calculated following Caswell (2001: 300).

Intra-annual patterns in demography

I evaluated intra-annual patterns in demography with a prospective perturbation analysis which involved calculation of elasticities of elements in periodic matrices $\mathbf{B}_{\mathbf{NB}}$ and $\mathbf{B}_{\mathbf{B}}$ (Caswell 2001). Periodic matrices used for prospective perturbation analyses were parameterized with mean demographic rates per population. Elasticity of a demographic rate indicates the degree to which population growth rate would be influenced for a small proportional change in that demographic rate, given that all other rates in the matrix are held constant (Caswell 2001).

Inter-annual patterns in demography

I evaluated inter-annual patterns in demography with retrospective perturbation analysis of periodic matrices which was done with life table response experiments

(LTRE; Caswell 2001, Keyfitz and Caswell 2005). LTREs compare the observed change in population growth rate between two or more matrices and decompose this difference into contributions from individual demographic rates, while simultaneously considering the sensitivities and observed changes of individual survival and fertility estimates. A contribution value for each demographic rate expresses this observed change in the rate and the realized influence on population growth rate. LTRE analysis is common in the literature (e.g., Levin et al. 1996, Dobson and Oli 2001), but an LTRE analysis for populations modeled with periodic matrices is rare. In populations described by an annual matrix model, population growth rate in one population (denoted $\lambda_a^{(\alpha)}$) can be approximated by the population growth rate in another population (denoted $\lambda_a^{(\beta)}$):

$$\lambda_a^{(\alpha)} \approx \lambda_a^{(\beta)} + \sum_{i,j} \left(a_{ij}^{(\alpha)} - a_{ij}^{(\beta)} \right) \left. \frac{\partial \lambda_a}{\partial a_{ij}} \right|_{\mathbf{A}^*} \qquad (1)$$

where

$$\mathbf{A}^* = \frac{\left(\mathbf{A}^{(\alpha)} + \mathbf{A}^{(\beta)} \right)}{2} . \qquad (2)$$

The (*i*,*j*)th summand in (1), namely

$$\left(a_{ij}^{(\alpha)} - a_{ij}^{(\beta)} \right) \left. \frac{\partial \lambda_a}{\partial a_{ij}} \right|_{\mathbf{A}^*} \qquad (3)$$

is called the contribution of the parameter a_{ij} to the change in λ between $\lambda_a^{(\alpha)}$ and $\lambda_a^{(\beta)}$ (Caswell 2001:261).

In the periodic construct, the annual transition matrix $\mathbf{A}_h$ is the product of *h* periodic matrices $\mathbf{B}_1, \mathbf{B}_2, ..., \mathbf{B}_{h-1}, \mathbf{B}_h$ where $\mathbf{B}_h$ is a matrix describing changes in a population over a time scale shorter than that of $\mathbf{A}_h$, hence:

$$\mathbf{A}_h = \mathbf{B}_1 \mathbf{B}_2 ... \mathbf{B}_{h-1} \mathbf{B}_h . \qquad (4)$$

Here the contribution c_{ijk} of the parameter b_{ijk} (i.e., the *i,j*th entry of the matrix $\mathbf{B}_k$) to the change in λ is defined by

$$c_{ijk} = \left(b_{ijk}^{(\alpha)} - b_{ijk}^{(\beta)} \right) \frac{\partial \lambda_a}{\partial b_{ijk}} \bigg|_{(\mathbf{B}_1^*, \mathbf{B}_2^*, ..., \mathbf{B}_k^*)} \qquad (5)$$

where

$$\mathbf{B}_k^* = \frac{(\mathbf{B}_k^{(\alpha)} + \mathbf{B}_k^{(\beta)})}{2} . \qquad (6)$$

Equation (6) indicates that contributions to population change are derived from a mean matrix of all matrices being compared.

This intra-annual periodic LTRE design also allows for comparison of demographic changes from year to year for studies conducted over a series of years, like the ones of Kabat and Thompson (1963) and Speake (1967). In this time sequential formulation, I used periodic matrices for year *t* as the reference (matrices with entries $b_{ijk}^{(\beta)}$ in equation [5]) to which periodic matrices for year *t+1* (matrices with entries $b_{ijk}^{(\alpha)}$ in equation [5]) were compared. This was done within each study population over all sequence of years in the respective studies. Thus, an individual contribution measurement reflects the degree to which a change in a demographic rate from year *t* to year *t+1* influenced the corresponding change in population growth rate between years *t* and *t+1*. I limited year to year comparisons to those within the chronological sequence of years in each study (e.g., 1960 as "reference" compared to 1961 as "treatment" for the Alabama population). I did not compare all year combinations (e.g., 1940 as "reference" compared to 1950 as "treatment" for the Wisconsin population) because the demographic rates in year *t+1* should be most influenced by the demographic rate structure in year *t*.

Inferences from LTRE analyses are typically made from individual contribution values describing the importance of changes in demographic rates between 2 conditions ("reference" and "treatment"). I, however, conducted multiple LTREs in a time sequential method for each population (n=9 and n=11 LTREs for Wisconsin and Alabama, respectively). This yielded a sequence of contribution values that describe the variability of influence certain demographic rates have on observed change in population growth rate. Before deriving inference from the sequences of contribution values it is important to recognize that these contributions reflect change in a purely deterministic matrix model (i.e., demographic rates were not functions of population size or other demographic rates). Thus, for an identical change in a particular demographic rate, an increase in that demographic rate will result in a positive contribution value to the observed change in population growth rate while a decrease in that demographic rate would lead to a negative contribution value. Through time for a stable population, the contribution value will be both negative and positive and an average contribution value would be near zero. This would mask the magnitude of influence of the demographic rate on observed changes in population growth rate. Thus, because both the Wisconsin and Alabama population were near stability during their respective time frames (Table 1), I took the absolute value of each contribution value and then calculated the mean contribution value per demographic rate and its associated 95% CI. This approach captures both inter-annual variation in demographic rates and sensitivity measurements, both of which are important aspects of demography to understand if a greater understanding of temporal variation is to be developed (Horvitz and Schemske 1995, Pfister 1998).

Results

Demographic rates estimated from Kabat and Thompson (1963) and Speake (1967) were similar to those reported in the literature (Table 1; Brennan 1999). Nonbreeding season survival of subadults and adults in the Wisconsin population was lower than that of the same demographic rate in the Alabama population (Table 1). Subadult and adult fertility in the Wisconsin population was higher than that of the Alabama population (Table 1). The λ_a of both populations ($\lambda_{\text{Wisconsin}} = 0.99$, $\lambda_{\text{Alabama}} = 1.12$) was reasonable and similar ($P(\lambda_{\text{Wisconsin}} = \lambda_{\text{Alabama}}) = 0.354$).

Intra-annual patterns in demography

Subadult survival during the nonbreeding season had the greatest potential influence on λ_a in both the Wisconsin and Alabama populations; however, elasticities for this particular demographic rate were greater in Wisconsin than in Alabama (Table 2). During the breeding season, subadult fertility and subadult survival collectively accounted for 84.3% and 74.4% in the Wisconsin and Alabama populations, respectively (Table 2). During the nonbreeding season, the elasticity of subadult survival is 5.37 and 3.03 times greater than adult survival in the Wisconsin and Alabama populations, respectively (Table 2).

Inter-annual patterns in demography

In the southern population, subadult fertility had the largest average contribution to the observed changes in population growth rate, while subadult survival in the nonbreeding season in this population was the second most influential demographic rate to observed changes in population growth rate (Table 2, Fig. 2). This pattern was reversed in the northern population. Subadult survival in the nonbreeding season had the largest average contribution value and subadult fertility had the second largest contribution value to observed change in population growth rate in the northern population. Beyond subadult fertility and subadult survival in the nonbreeding season in both populations, other demographic rates in both populations had relatively little influence on changes in population growth rate and their level of influence was consistently nominal (Fig. 2). Confidence intervals for the contributions of demographic rates were wide which suggests that the influence of changes in a demographic rate to observed changes in population growth rate can vary from year to year.

Discussion

Intra-annual patterns in demography

A focus of life history theory is to identify patterns in demography and understand the significance of such relationships to evolution of life histories (Stearns 1992, Roff 2002) and efficacy of conservation efforts (Lima et al. 2003, Sæther et al. 2005). A major advancement in this arena has been the concept that elasticities of demographic rates vary predictably across life histories. For instance, λ_a of species characterized by low annual fertility and high annual survival ("slow" species) should be most influenced by changes in adult survival (Heppell et al. 2000, Sæther and Bakke 2000). At the other end of the spectrum (i.e., low annual survival and high annual fertility, "fast" species), subadult fertility should most influence population growth. This pattern, however, has been developed with prebreeding matrix population models with an annual time step (Heppell et al. 2000, Sæther and Bakke 2000). Thus, fertility estimates in these studies represent fecundity (i.e., physiological maximum reproductive output) decremented by subadult survival over an annual cycle. Similar to these studies with an annual time step, fertility of subadult bobwhites has the highest elasticity when the populations are evaluated with an annual model (*T. H. Folk, unpublished data*).

An implicit assumption of the annual construct is that survival rates do not vary appreciably through the year. This is likely not the case for numerous species (Lima et al. 2003), and certainly not for bobwhites (Curtis et al. 1988). Thus when matrix models are constructed to reflect a more accurate representation of demographic rate variation, the λ_a of bobwhites in our northern and southern bobwhite population is most influenced by subadult survival in the nonbreeding season, not subadult fertility as the annual model suggests and life history theory might predict. Our results are consistent with those of Sæther and Bakke (2000) and others in that demographic attributes early in life have the greatest potential influence on λ_a. Our approach, however, evaluated the intra-annual variation in influence of this demographic rate, and demonstrated that survival early in life and not fecundity had the greatest potential influence on λ_a.

Inter-annual patterns in demography

I employed LTRE analysis in 2 novel ways to investigate how bobwhite populations change seasonally from one year to another. First, the use of LTRE analyses of periodic matrices gives a more detailed picture of demography of a species through out the annual cycle. Second, evaluation of the contribution values through time, as done with time sequential LTREs, can reveal aspects of demographic stability and influence of particular demographic rates. To our knowledge, both the consideration of average and seasonal contributions is a novel interpretation of retrospective analyses, and can improve our knowledge of the influence of demographic seasonality in animal population dynamics.

Average contribution estimates indicated that the demographic force behind population change differed between the northern and southern bobwhite population. In the southern population, fluctuations in subadult fertility had the greatest average contribution to population change, while in the northern population changes in subadult survival in the nonbreeding season had the greatest average influence on population growth. Additionally, these 2 demographic rates also varied the most as compared to other contribution measurements within populations. These differing results support several ideas about bobwhite biology. First, it has long been supposed that dry, hot summers can be detrimental to bobwhite nesting effort, especially in southern portions of its range (Brennan 1999). In fact, Guthery et al. (2001) recently demonstrated that bobwhites in Texas cease reproduction above temperatures of 39.2 C°. In the northern population, mean high temperature during the breeding season (June to August) was 31.1 C° (1951) while in the southern population it was 37.2 C° (1963; www.ncdc.noaa.gov). Conversely, bobwhite populations in these northern portions of its geographic range face severe winters where survival can be depressed due to limited food availability, increased predation risk, and exposure to low temperatures (Errington and Hamerstrom 1936). These conditions are experienced with less frequency at southern latitudes. The results of our time sequential LTRE analysis are supportive of these varying environmental processes. Efficacy of conservation efforts for bobwhites can be increased with a consideration of the temporal variability in bobwhite demography.

Lima et al. (2003) suggested that temporal variability is recognized as a central aspect in small mammal demography, but that its incorporation into population models is rare. There exists a similar lack of understanding of seasonality in avian demography, especially for species of conservation concern. Similar to Lima et al.'s (2003) investigation of several rodent species, our investigation into northern bobwhite population dynamics demonstrates that incorporation of seasonality into population models can be important to understanding the population dynamics of a species. Even further, understanding how seasonality of demographic rates change across years can increase our understanding of a species' population dynamics (Horvitz and Schemske 1995, Pfister 1998) and improve efficacy of conservation efforts (Cooch et al. 2001, Lima et al. 2003).

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Table 1. Parameter estimates associated with periodic matrix models of northern bobwhite populations in Wisconsin (1942-1951) and Alabama (1951-1963). Asymptotic population growth rate (λ_a) was determined from a periodic matrix model populated with mean demographic rate estimates for Alabama and Wisconsin separately.

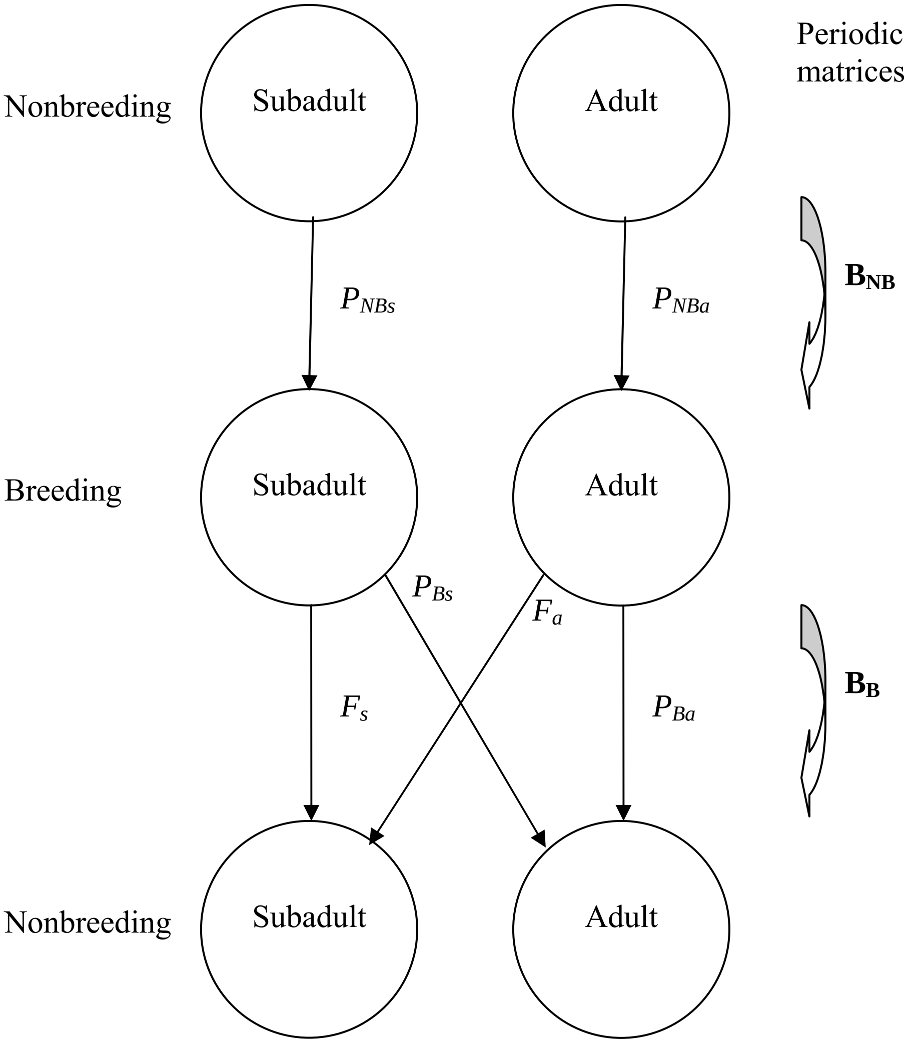
	Wisconsin			Alabama		
	Mean	Lower 95% CI	Upper 95% CI	Mean	Lower 95% CI	Upper 95% CI
Subadult nonbreeding survival	0.418	0.262	0.574	0.713	0.587	0.838
Adult nonbreeding survival	0.418	0.262	0.574	0.713	0.587	0.838
Subadult fertility	1.986	1.488	2.484	1.183	0.658	1.708
Adult fertility	1.986	1.488	2.484	1.183	0.658	1.708
Subadult breeding survival	0.371	0.218	0.523	0.391	0.256	0.526
Adult breeding survival	0.371	0.218	0.523	0.391	0.256	0.526
λ_a	0.985	0.619	1.351	1.122	0.781	1.463

Table 2. Elasticity and contribution measurements from periodic matrix models describing northern bobwhites in Wisconsin (1942-1951) and Alabama (1951-1963). Elasticity measurements are from a periodic matrix model of mean demographic rates for either the Alabama or Wisconsin population. Mean contribution estimates were calculated from all contribution measurements when life table response experiments compared year *t+1* to year *t* across all years of the respective study (see Methods for further explanation).

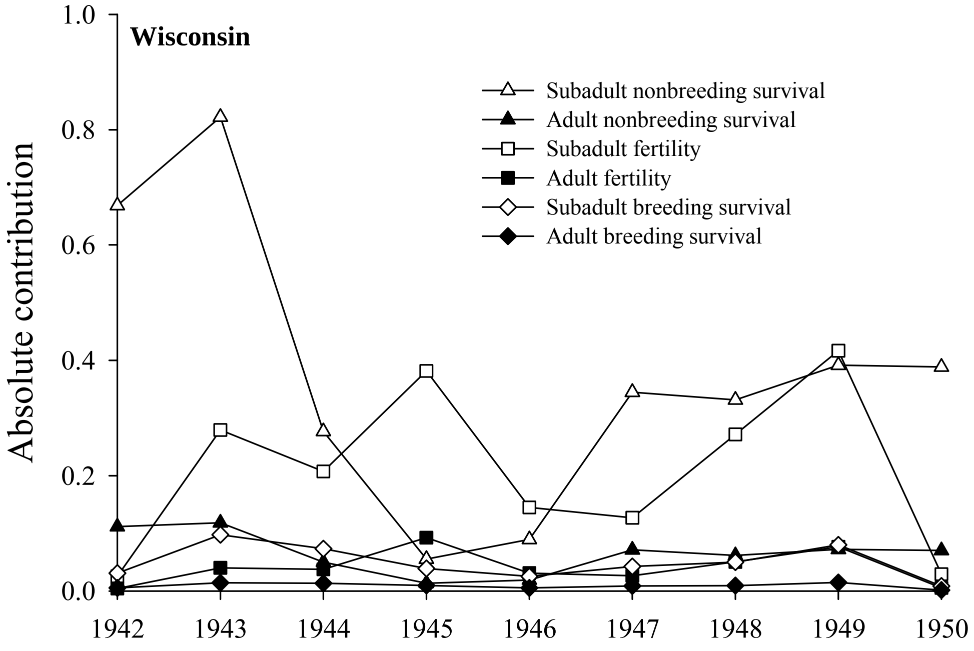
	Wisconsin				Alabama			
		Contribution				Contribution		
	Elasticity	Mean	Lower 95% CI	Upper 95% CI	Elasticity	Mean	Lower 95% CI	Upper 95% CI
Subadult nonbreeding survival	0.843	0.479	0.153	0.806	0.752	0.265	0.04	0.525
Adult nonbreeding survival	0.157	0.087	0	0.270	0.248	0.099	0	0.276
Subadult fertility	0.710	0.296	0	0.594	0.559	0.328	0.050	0.605
Adult fertility	0.133	0.060	0	0.214	0.185	0.115	0	0.303
Subadult breeding survival	0.133	0.066	0	0.228	0.185	0.142	0	0.349
Adult breeding survival	0.025	0.013	0	0.085	0.061	0.051	0	0.182

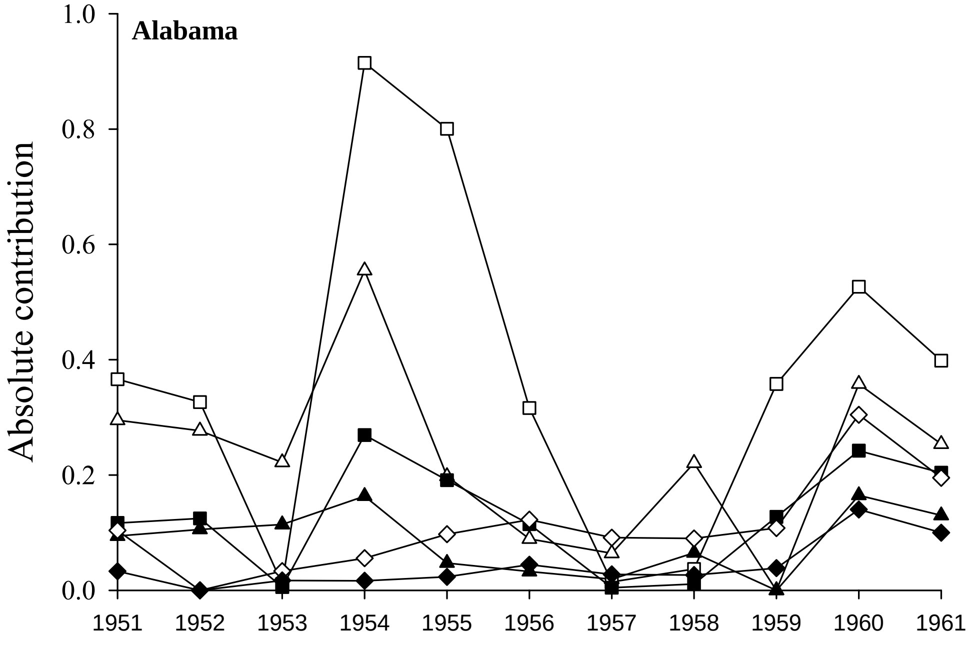
Fig. 1. Life cycle graph representing northern bobwhites. The annual cycle is divided into a breeding (2 April-15 November) and nonbreeding (16 November-1 April) season with both seasons divided between subadults (i.e., individuals in their first year of life) and adults (i.e., individuals post subadult stage).

Fig. 2. Patterns of temporal changes in demographic rate contributions to changes in population growth rate for northern bobwhite populations in Wisconsin and Alabama. Absolute contribution values for a demographic rate in year *t* represent the magnitude of the contribution to the change in population growth rate from that year *t* to year *t+1*.



Periodic matrices
Nonbreeding
Subadult
Adult
P_{NBs}
P_{NBa}
$\mathbf{B}_{\mathbf{NB}}$
Breeding
Subadult
Adult
P_{Bs}
F_a
F_s
P_{Ba}
$\mathbf{B}_{\mathbf{B}}$
Nonbreeding
Subadult
Adult


Wisconsin
Absolute contribution
0.0
0.2
0.4
0.6
0.8
1.0
1942
1943
1944
1945
1946
1947
1948
1949
1950
Subadult nonbreeding survival
Adult nonbreeding survival
Subadult fertility
Adult fertility
Subadult breeding survival
Adult breeding survival


Alabama
Absolute contribution
0.0
0.2
0.4
0.6
0.8
1.0
1951
1952
1953
1954
1955
1956
1957
1958
1959
1960
1961

APPENDIX. THE GEOMETRY OF POPULATION DYNAMICS AND MULTIVARIATE PERTURBATION ANALYSES IN MATRIX POPULATION MODELS

INTRODUCTION

Development of a greater understanding of species' population dynamics has long been a central focus of ecology (Kingsland 1985). Guided by several seminal papers, numerous studies have examined how biotic (e.g., food resources; Lack 1954) and abiotic (e.g., weather; Andrewartha and Birch 1954) factors influence individual vital rates (e.g., survival, fertility, age at maturity, etc.), which have greatly added to our understanding of population biology. More recently, population biologists have become interested in how multiple vital rates within a life history collectively interact to affect population dynamics, and how they are simultaneously shaped by natural selection (Horvitz and Schmeske 1995, Pfister 1998, Roff 2002, Morris and Doak 2004). For example, increased population growth rate of a colonizing species could reflect a recent increase in fertility and juvenile survival which might both be attributable to increased availability of resources (e.g., Parker 2000). The evolution of life histories is similarly guided by natural selection on multiple vital rates, simultaneously (Roff 2002, Coulson et al. 2003).

Understanding how the interplay of multiple vital rates influence a species evolution and amenability to anthropogenic management can lead to a better understanding of life history theory and population dynamics.

Matrix population models have become popular for developing and testing hypotheses about population dynamics and life history evolution (Leslie 1945, van Groenendael et al. 1988) because they are easier to use than differential equations and the biology of many species can easily be reflected in a matrix population model (Caswell 2001). In addition, matrix population models can easily be used to conduct perturbation analyses (e.g., sensitivity and elasticity analyses) for the purpose of measuring how parameters like asymptotic population growth rate, λ_1, are influenced by change in an underlying vital rate. For example, Brault and Caswell (1993) used a matrix population model to demonstrate that the population growth rate of killer whales (*Orcinus orca*) is most sensitive to a change in adult survival, with changes to fertility levels having less of an effect. Information of this type, both at the intra- and inter-specific levels, can further insights into life history theory (Franco and Silvertown 1997, Pfister 1998, Heppell et al. 2000, Sæther and Bakke 2000) and could increase the efficacy of management actions (Wisdom and Mills 1997, Flint et al. 1998, Mills and Lindberg 2002, Morris and Doak 2002, Koons et al. 2005).

A basic assumption of analytical perturbation analysis of matrix population models is that the sensitivity (or elasticity) of population growth rate to change in a particular vital rate is assessed when all other vital rates are held constant (Caswell 1978, 2001, Mills and Lindberg 2002; but see van Tienderen 1995 for solutions to instances when covariance exists among vital rates). This simplifying assumption may allow identification of the vital rate with the single greatest functional influence on population growth rate, but it ignores the biological reality that multiple vital rates change simultaneously through time to influence population dynamics (Horvitz and Schemske 1995, Pfister 1998, Chapter V), which could ultimately affect evolutionary change (Lande 1982, Roff 2002). Evaluation of multiple, simultaneous vital rate perturbations will incorporate another layer of reality in perturbation analysis of matrix population models and thus increase our ability to understand more realistic patterns in population dynamics.

In a seminal article, Lande (1982) developed the quantitative framework of Robertson's (1966) influential secondary theorem of natural selection which describes how a trait may respond to multiple sources of selection. Lande's (1982; and Lande and Arnold 1983) analytical advancement provided quantitative geneticists a tool for measuring the effects of multivariate selection pressures on evolutionary change. More recently, Rice (2002) has built upon Lande's work (1982; and Lande and Arnold 1983) to create a deeper understanding of developmental evolution of phenotypic traits. Both the approach of Lande (1982) and Rice (2002) utilize a visual, heuristic tool analogous to Wright's (1932) adaptive topography or fitness landscape. Conceptualization (Wright 1932, Brodie et al. 1995, Gavrilets 2004) and quantification (Lande 1982, Rice 2004) of multivariate phenomenon in nature has provided new tools for refinement and evaluation of theories underlying evolutionary processes. Integrating these tools into population dynamics and life history theory will advance these fields as well. In this paper, I extend

Lande (1982) and Rice's (2002) approach into the matrix population model framework so that it can easily be used to address any type of multivariate demographic question (e.g., applied management, demographic, evolutionary, etc.). First, I describe a visual geometrical tool, similar to that of Wright (1932), Rice (2002), and Gavrilets (2004). Second, from this geometrical tool and Lande's (1982) version of the secondary theorem of natural selection, I introduce several mathematical tools that quantify the influence of simultaneous perturbations to multiple demographic parameters of a matrix population model on asymptotic population growth rate, λ_1. I then present examples ranging from intraspecific management scenarios to interspecific evaluations of life history patterns to demonstrate the utility of this set of visual and mathematical tools. Finally, I discuss some of the assumptions of this approach, and the extent of inference that can be drawn in population dynamics and studies of life history.

GEOMETRY OF DISCRETE TIME POPULATION MODELS

Development of visual, heuristic tools in the areas of quantitative genetics and developmental evolution, such as fitness surfaces (Wright 1932) and phenotypic landscapes (Rice 2002), have allowed for a more intuitive understanding of the complex relationships under investigation (Phillips and Arnold 1989, Schluter and Nychka 1994, Brodie et al. 1995). An analogous tool has not been developed for use in population dynamics, despite the mathematical similarities amongst the fields (cf. Caswell 1978 with Lande and Arnold 1983). In this section, I describe a visual geometric tool for improving the understanding of demography described by matrix population models. I will refer to this visual representation of demography as a *demographic landscape*.

Fitness landscapes, in general, are composed of a multidimensional surface where the topography of the surface describes the interaction of the underlying genetic or phenotypic factors that influence some aspect of fitness (Brodie et al. 1995, Rice 2002, Arnold 2003, Gavrilets 2004). The function that describes this surface can be composed of the genetic heritabilities, covariance measures between genetic and phenotypic traits, etc. An excellent example of an adaptive landscape can be seen in Schluter and Nychka (1994; e.g., Figure 3). Here Schluter and Nychka (1994) utilized an adaptive landscape approach to evaluate the response of overwinter survival of song sparrows (*Melospiza melodia*) to natural selection on 6 morphological traits. This potentially complex function has as the response variable some metric of fitness (Gavrilets 2004, Rice 2004), such as overwinter survival in the Schluter and Nychka (1994) adaptive landscape. Thus, movement across the fitness landscape can describe how combinations of genotypic, phenotypic, and environmental factors combine to influence fitness of individuals within a species. Although population growth rate is an appropriate measure of evolutionary fitness (Charlesworth 1980, Lande 1982, McGraw and Caswell 1996, Oli 2003), the analogy to demographic models has not been presented (but see Lande 1982 for the theoretical foundation for such an approach). Furthermore, a geometrical representation of matrix population models has not been described, but could help answer many applied and evolutionary questions in population biology and life history theory.

To develop the simplest demographic landscape, consider a population that is closed to immigration and emigration, and annual survival and fertility are constant across individuals. Using these assumptions, just 2 vital rates determine population growth rate:

$$\lambda = S(1+F)$$

where λ is the annual population growth rate, S is the annual survival rate of individuals in the population, and F is fecundity (i.e., birth rate). This function can easily be expressed as a surface across all ranges of S and F; however, not all survival and fecundity combinations are realized as an actual species in nature with that demography (e.g., a hypothetical species with $S = 0.05$ and $F = 0.05$ would rapidly become extinct). Rather, within taxonomical classes, survival and birth rates covary in predictable patterns (squamate reptiles: Dunham and Miles 1985; birds: Sæther 1988; mammals: Stearns 1983) For example, several authors (Sæther 1988, Harvey et al. 1989, Gaillard et al. 1989, Promislow and Harvey 1990) have suggested that vertebrate life histories exist around a "slow-fast" continuum where slow species are typified by late maturation, high annual survival, and production of few offspring whereas fast species have high annual survival, early maturation, and produce numerous offspring.

Incorporation of interspecific patterns of covariation between survival and fecundity will restrict the landscape to regions where life histories are known to exist. Thus, Figure 1 represents a theoretical demographic landscape of the closed, unstructured population model given above, yet is limited to regions known to exist for the range of vertebrate life histories. Interpretation of this demographic landscape is analogous to that of fitness landscapes relating individual characters to a fitness component. For example, position *P0* in Figure 1 is described by $S = 0.75$, $F = 0.34$, and thus $\lambda = 1.0$. If that point were projected onto the surface of the demographic landscape it would indicate that proportional changes in *F* would lead to the greatest change in λ, as compared to identical proportional changes in *S* $\left(e.g., \left[\frac{F}{\lambda} \frac{\partial \lambda}{\partial F} \right] > \left[\frac{S}{\lambda} \frac{\partial \lambda}{\partial S} \right] \right)$. Conversely, point *P1*, where $S = 0.25$, $F = 3.0$, and thus $\lambda = 1.0$, indicates that proportional perturbations to *S* would lead to greatest change in λ, as compared to identical proportional changes in *F* $\left(e.g., \left[\frac{S}{\lambda} \frac{\partial \lambda}{\partial S} \right] > \left[\frac{F}{\lambda} \frac{\partial \lambda}{\partial F} \right] \right)$. In an evolutionary interpretation, the hypothetical life history and point *P0* would respond more quickly to natural selection operating through fecundity than survival. This contrasts with the hypothetical life history at point *P1*, where the patterns in selection pressures are reversed between survival and fecundity. This approach is analogous to sensitivity and elasticity analyses that are conducted with matrix population models, and identifies the vital rate with the greatest potential influence on the value of λ. Although this initial example is simplistic, conceptualization of actual population dynamics can follow from this illustration.

Often, population dynamics cannot be described by such a simple model. Rather, age or stage structure is frequently important and should be reflected in the population model, especially if rigorous inference is to be drawn. Demographic landscapes can easily be developed from matrix population models. From a matrix population model $\mathbf{A}$ that describes a particular life history, I are able to construct a polynomial that will express λ as a function of survival and fertility rates. The function describing the demographic landscape of that life history is obtained from the characteristic equation of matrix $\mathbf{A}$:

$$\lambda_1(a_{11},..,a_{ij},..,a_{mm}) = Det(\lambda_i\mathbf{I} - \mathbf{A}) \quad (1)$$

where $\mathbf{I}$ is the identity matrix of same dimension as $\mathbf{A}$ and $Det(\lambda_i\mathbf{I} - \mathbf{A})$ is the determinant of the matrix resulting from the relation of $\mathbf{I}$ to $\mathbf{A}$. This characteristic equation will consist of $m+1$ variables where m variables represents the number of demographic parameters incorporated into $\mathbf{A}$. This may equal at a minimum the number of matrix level entries or at a maximum the number of lower-level parameters considered (e.g., a fertility element in matrix $\mathbf{A}$ may be expressed as fecundity decremented by measures of survival like nesting success, survival to weaning, etc.). The additional parameter beyond the m demographic variables (i.e., $m+1$) is the set of eigenvalues that solve the characteristic equation. Since λ_1 is a root (i.e., an eigenvalue) of the characteristic equation of $\mathbf{A}$, λ_1 is a function of the m variables. The graph of this function is a $m+1$ dimensional hypersurface, which I refer to as the demographic landscape of matrix $\mathbf{A}$.

Lande (1976, 1979; Lande and Arnold 1983; Arnold 2003) suggested that the use of adaptive landscapes in understanding evolution of phenotypic traits rests on 3 main assumptions: a) phenotypic traits are normally distributed, b) fitness of individuals is independent, or nearly independent c) the function that determines fitness values should be continuous and smooth. In our development of a demographic landscape I will assume the same, but the biology of some species may not fit this construct (e.g., differences in patterns of mating systems, form of density dependence operating within a species).

The relatively simple demographic landscape presented in Figure 1 was chosen because it could easily be represented in a three dimensional form. However, the interpretation of a demographic landscape can be complicated by the dimension of a matrix population model, or number of vital rates being considered. Nevertheless, the conceptual and mathematical utility of a demographic landscape still exists in higher dimensions.

DIRECTIONAL DERIVATIVES AND THE GRADIENT VECTOR

The utility of demographic landscapes is highlighted by the use of perturbation analyses. Traditional perturbation analysis of matrix population models (i.e., partial derivatives) was first presented by Caswell (1978) where he provided the algebraic solutions to the sensitivity of λ_1 to a change in any entry $a_{i,j}$ of $\mathbf{A}$ $\left(i.e., {}^{\partial \lambda_1}\!\big/_{\partial a_{ij}} \right)$, where $a_{i,j}$ represents the transition rate from the *j*th stage to the *i*th stage. Caswell's (1978) presentation considers the effect of perturbing a single $a_{i,j}$ element while all others are held constant. Frequently it is desired to understand the influence of multiple, simultaneous perturbations to vital rates. This has been accomplished via manual perturbation where vital rates themselves are changed manually and the resulting effect on λ_1 evaluated (Cross and Beissinger 2001). This approach is not preferable though because there is no standardized perturbation amount, making it difficult to compare results across studies (Mills and Lindberg 2002). Van Tienderen (1995) provides the solution to a perturbation analysis when covariance between vital rates is known and quantified; however, knowledge of the full variance-covariance structure of vital rates for a particular species is rarely known. In addition, van Tienderen's (1995) approach does not include situations when vital rates do not co-vary with one another, but are perturbed simultaneously. By extending Lande's (1982) use of the gradient into the realm of matrix population models, I present here a perturbation analysis that allows for multiple, simultaneous changes in vital rates, is easily understood within the framework of the demographic landscape, and does not require knowledge of the variance-covariance structure of a particular life history. I consider a *directional derivative* as the metric that evaluates the influence of multiple, simultaneous perturbations in vital rates to changes in λ_1.

Throughout this presentation, I assume use of a linear, time invariant matrix population model. For simplicity I only present computation of the directional derivative with respect to λ_1. However, I note that the influence of vital rate perturbations can be assessed on a variety of matrix model attributes (e.g., stable age distribution, momentum, damping ratio, etc.).

On an $m+1$ dimensional demographic landscape of matrix $\mathbf{A}$, a directional derivative represents the change in λ_1 relative to movement in a given direction across the demographic landscape. On this demographic landscape, traditional sensitivity and elasticity measurements (*sensu* Caswell 1978, de Kroon et al. 1986) measure the rate of change in λ_1 for movement with respect to one axis. To develop the notion of a directional derivative completely, assume a species with a particular set of vital rates (expressed as a matrix $\mathbf{A}$) is represented by a point $P_0(a_{11},..,a_{ij},..,a_{mm})$ within the demographic landscape of a matrix $\mathbf{A}$. Directional derivatives quantify the influence on λ_1 of absolute (sensitivity) or proportional (elasticity) perturbations to the vital rates of a given life history (i.e., $P_0[a_{11},..,a_{ij},..,a_{mm}]$) towards some new position $P_1(a_{11}+\delta_{11},..,a_{ij}+\delta_{ij},..,a_{mm}+\delta_{mm})$, where δ_{ij} represents increases or decreases in a particular vital rate which corresponds to movement along the demographic surface with respect to element a_{ij}.

Movement from position P_0 towards position P_1 can be represented by a vector $\mathbf{a}$ which originates at position P_0 and ends at P_1. This vector $\mathbf{a}$ represents a series of perturbations to vital rates of matrix $\mathbf{A}$. Thus, the vector $\mathbf{a}=\left\langle \delta_{11},..,\delta_{ij},..,\delta_{mm}\right\rangle$ represents the change in the pertinent $a_{i,j}$ or lower-level vital rates of the a_{ij}. In computation of the directional derivative, it is preferable to compute movement in a chosen direction ($\mathbf{a}$) over a uniform distance. To accomplish this, I simply use the unit vector $\mathbf{u}=\dfrac{\mathbf{a}}{\|\mathbf{a}\|_2}$ in place of $\mathbf{a}$ (where $\|\mathbf{a}\|_2$ is the 2-norm or Euclidean norm; Stewart 1995). An entry of vector $\mathbf{a}$ can represent the desired change in that vital rate, whether it is an increase or a decrease. Any vector $\mathbf{a}$ can then easily be converted to a unit vector $\mathbf{u}$. Rarely though can populations be managed with such efficiency that vital rates can be perturbed by an exact and predicted amount. To reflect this reality, I compose our vector $\mathbf{a}$ representing unit changes in a vital rate. Thus, if only the *ij*th value was to be modified, vector $\mathbf{a}$ would appear as $\mathbf{a} = \left\langle a_{11}, .., a_{ij}, .., a_{mm} \right\rangle = \left\langle 0, .., 1, .., 0 \right\rangle$. If multiple, simultaneous perturbations were to be considered, each element to be perturbed would contain a 1. Further, the direction of perturbation can be indicated. The previous vector, with 1 as the only non-zero component, indicates that the vital rate in the *ij*th position will be increased. If a decrease in this vital rate is desired, a -1 would be used. It is also possible to evaluate the simultaneous increase and decrease of separate vital rates (see intraspecific example for illustration of this point). This assumption, namely perturbation of a vital rate by unit amounts is identical to the assumption of traditional sensitivity analyses (Caswell 2001).

Given a unit vector $\mathbf{u}$ that describes a set of perturbations to a particular life history, the directional derivative, $D_{\mathbf{u}}\lambda_1$, of λ_1 in the direction of $\mathbf{u}$ is given by

$$D_{\mathbf{u}}\lambda_1 = \nabla\lambda_1 \bullet \mathbf{u}, \tag{2}$$

where $\nabla\lambda_i$ is the gradient of λ_i. Thus, the directional derivative $D_{\mathbf{u}}\lambda_1$ is the quantity given by the dot product of the gradient vector and $\mathbf{u}$. The gradient vector is simply a vector with individual entries being the partial derivatives of λ_1 with respect to a_{ij} or lower-level vital rates of the a_{ij}. Furthermore, the gradient vector can represent either sensitivity calculations

$$\nabla_s\lambda_1 = \left\langle \frac{\partial\lambda_1}{\partial a_{11}}, .., \frac{\partial\lambda_1}{\partial a_{ij}}, .., \frac{\partial\lambda_1}{\partial a_{mm}} \right\rangle \tag{3}$$

or elasticities

$$\nabla_e \lambda_1 = \left\langle \frac{a_{11}}{\lambda_1}\frac{\partial \lambda_1}{\partial a_{11}},..,\frac{a_{ij}}{\lambda_1}\frac{\partial \lambda_1}{\partial a_{ij}},..,\frac{a_{mm}}{\lambda_1}\frac{\partial \lambda_1}{\partial a_{mm}} \right\rangle . \tag{4}$$

Note the subscripts ∇_s and ∇_e in equations 3 and 4 which I use to denote whether the gradient vector is composed of sensitivities or elasticities, respectively.

It should be noted that a traditional sensitivity or elasticity measurement (*sensu* Caswell 1978) is merely a special case of the directional derivative, namely when $\mathbf{u}$ is of the form $\mathbf{u} = \left\langle 0_{11},..,1_{ij},..,0_{mm} \right\rangle$ (Stewart 1995). Additionally, while the directional derivative in the direction of the gradient (equation 2) gives the maximal increase in λ_1, the directional derivative in the opposite direction of the gradient, that is $-\nabla\lambda_1$, gives the maximal decrease in λ_1. Movement in the direction of the gradient on the demographic landscape corresponds to the set of perturbations that would lead to the greatest increase in λ_1. The choice of whether to maximize the increase or decrease in λ_1 will depend on the nature of the question at hand (e.g., evolutionary fitness versus control of pest populations).

Further, the gradient vector can be composed of second derivatives (i.e., $\frac{\partial^2 \lambda_1}{\partial a_{ij}^2}$; Caswell 1996). In this case the gradient vector indicates the direction of movement across the demographic landscape that would lead to the greatest change in the shape of the local area on the demographic landscape for a given life history. To clarify, a gradient vector composed of first-derivatives will be denoted as $\nabla_s \lambda_1$, and a gradient vector composed of second derivatives will be denoted as $\nabla_s^2 \lambda_1$. Gradient vectors composed of first- and second-derivatives have important evolutionary interpretations as well (Caswell 1996, Rice 2004).

EXAMPLES OF DIRECTIONAL DERIVATIVES, THE GRADIENT VECTOR, AND THEIR GEOMETRICAL INTERPRETATION

Directional derivatives, the gradient vector, and demographic landscapes have utility in applied population management, interspecific life history investigations, and potentially many other contexts. Here I pose questions related to the aforementioned topics and present the application of the directional derivative, gradient vector, and demographic landscape to answer these questions. In the intraspecific example I evaluate how the directional derivative is affected by different demographic perturbations that would correspond to different management scenarios. In the interspecific example, I instead focus on how the gradient vector itself changes across several vertebrate species. Although these two examples utilize the same mathematical approach, I pose very different questions within each example.

Directional derivatives in an applied population management scenario

Population managers are frequently faced with management decisions that will simultaneously influence multiple vital rates, but, as was previously mentioned, the common perturbation techniques applied to matrix population models only evaluate perturbation to individual vital rates. Consider the lesser snow goose (*Anser caerulescens*), an avian game species whose populations have increased dramatically in recent years (Cooch et al. 1989, Cooke et al. 1995) to the point that breeding ground habitats are rapidly being degraded (Hik and Jeffries 1990, Hik et al. 1991, Williams et al. 1993). Wildlife agencies are charged with control of these populations, and because of the recent, rapid growth in populations of this species, management scenarios will likely be geared towards reduction of multiple vital rates. Thus, it is the goal of wildlife managers to decrease the population growth rate of lesser snow geese (i.e., management actions geared towards decreasing the directional derivative value).

To explore the impact of multiple, simultaneous vital rate perturbations to lesser snow goose population growth rate, I utilize the pre-breeding, matrix population model in Cooch et al. (2001), which I populate with mean vital rates of the lesser snow goose population at La Pérouse Bay, Manitoba from 1973 to 1990. In general, Cooch et al.'s (2001) annual matrix takes the form

$$\mathbf{A}_{LESG} = \begin{bmatrix} 0 & \gamma_2 B_2 S_{\mathbf{Y}} \eta_{\mathbf{Y}} & \gamma_3 B_3 S_{\mathbf{Y}} \eta_{\mathbf{Y}} & \gamma_4 B_4 S_{\mathbf{Y}} \eta_{\mathbf{Y}} & \gamma_5 B_5 S_{\mathbf{Y}} \eta_{\mathbf{Y}} \\ S_{\mathbf{A}} \eta_{\mathbf{A}} + I & 0 & 0 & 0 & 0 \\ 0 & S_{\mathbf{A}} \eta_{\mathbf{A}} + I & 0 & 0 & 0 \\ 0 & 0 & S_{\mathbf{A}} \eta_{\mathbf{A}} + I & 0 & 0 \\ 0 & 0 & 0 & S_{\mathbf{A}} \eta_{\mathbf{A}} + I & S_{\mathbf{A}} \eta_{\mathbf{A}} + I \end{bmatrix}$$

where $S_{\mathbf{A}}$ and $S_{\mathbf{Y}}$ are adult and yearling survival, respectively; $\eta_{\mathbf{A}}$ and $\eta_{\mathbf{Y}}$ are adult and yearling fidelity, respectively, to the La Pérouse Bay breeding grounds; I is the immigration rate; γ_i is the age specific breeding propensity; and B_i is the age specific breeding success (see Cooch et al. 2001 for details on mark-recapture estimation of these parameters). Parameter estimates are given in Table 1. Because this population model includes parameters that describe an open population (i.e., immigration and site fidelity are incorporated into the matrix), the effect of hypothetical management scenarios are necessarily limited to describing the impact on the population growth rate of the La Pérouse Bay population.

Given a mathematical framework to assess the influence of multiple, simultaneous perturbations to vital rates (i.e., the directional derivative), I constructed several hypothetical management scenarios that range from the traditional perturbation analysis of vital rates in isolation (*sensu* Caswell 1978) to consideration of the set of perturbations that would lead to the greatest change in λ_1. Between these two extremes, I consider more biologically plausible management scenarios which involve perturbation of multiple vital rates. Further, our management scenarios consider simultaneous increases to some vital rates and decreases to other vital rates. The management scenarios are as follows:

1) *Perturbation to each vital rate separately*. This represents the results of traditional perturbation analysis and provides a point of comparison for directional derivatives computed from multiple, simultaneous perturbations.

2) *Decreases in breeding success and yearling survival across all age classes* (i.e., decreases in B_i and $S_{\mathbf{Y}}$). Extensive habitat degradation has occurred in and around the La Pérouse Bay breeding grounds (Hik and Jeffries 1990, Hik et al. 1991, Williams et al. 1993). Decreases in habitat quality can lead to depressed gosling and yearling survival

(Cooch et al. 1991, Francis et al. 1992, Williams et al. 1993). While not the result of a direct management action, managers may utilize natural depression of gosling and yearling survival in their efforts to decrease the size of the La Pérouse Bay population.

3) *Decreases in annual survival rate of yearlings and an increase in immigration rate* (i.e., decrease $S_{\mathbf{Y}}$ and increase I). Management actions geared towards modifying the demography of a game species commonly manipulate harvest limits (Calvert and Gauthier 2005). In the presence of hunter harvest, decreased gosling body condition due to poor quality breeding grounds can lead to reduced winter survival in younger geese (Hill et al. 2003). In the presence of additive harvest mortality, this may result in fewer yearling females returning to the La Pérouse Bay breeding grounds. Hypothetically, a reduction in recruitment of locally-reared females may permit regeneration of vegetation in and around the breeding grounds, and in turn, lead to a greater immigration rate into the La Pérouse Bay population.

4) *Decrease annual survival rate of adults across all age classes and increase immigration rate* (i.e., decrease $S_{\mathbf{A}}$, increase I). Perturbation to vital rates can in turn influence the effect of density dependent processes. Reduction in adult survival may lead to improved breeding ground habitat conditions because fewer philopatric females are returning to the breeding grounds. This in turn may increase availability of resources, which could lead to greater rates of immigration into the La Pérouse Bay breeding grounds.

5) *Decrease and increase all vital rates in proportion to the gradient vector*. While an unlikely management scenario, it does represent the set of perturbations (i.e., the

gradient vector itself) which would lead to the greatest positive and negative change in λ_1.

Computation of the directional derivative for each of these hypothetical scenarios follows from equation 2. Because all management scenarios are based on modification of the demography present in $\mathbf{A}_{LESG}$, the gradient vector, $\nabla_s \lambda_{1(LESG)}$, used for all scenarios is identical, and takes the following form:

$$\nabla_s \lambda_{1(LESG)} = \left\langle \frac{\partial\lambda}{\partial S_{\mathbf{A}}}, \frac{\partial\lambda}{\partial \eta_{\mathbf{A}}}, \frac{\partial\lambda}{\partial I}, \frac{\partial\lambda}{\partial S_{\mathbf{Y}}}, \frac{\partial\lambda}{\partial \eta_{\mathbf{Y}}}, \frac{\partial\lambda}{\partial \gamma_2}, \frac{\partial\lambda}{\partial \gamma_3}, \frac{\partial\lambda}{\partial \gamma_4}, \frac{\partial\lambda}{\partial \gamma_5}, \frac{\partial\lambda}{\partial B_2}, \frac{\partial\lambda}{\partial B_3}, \frac{\partial\lambda}{\partial B_4}, \frac{\partial\lambda}{\partial B_5} \right\rangle = \ldots$$
$$\ldots = \langle 0.93, 0.88, 1.05, 0.26, 0.19, 0.02, 0.02, 0.02, 0.10, 0.01, 0.02, 0.02, 0.09 \rangle.$$

More specifically, if I consider the set of perturbations suggested in scenario 3, the vector $\mathbf{a}$ representing a decrease in yearling survival and an increase in the immigration rate would take the following form:

$$\mathbf{a} = \langle \delta S_{\mathbf{A}}, \delta\eta_{\mathbf{A}}, \delta I, \delta S_{\mathbf{Y}}, \delta\eta_{\mathbf{Y}}, \delta\gamma_2, \delta\gamma_3, \delta\gamma_4, \delta\gamma_5, \delta B_2, \delta B_3, \delta B_4, \delta B_5 \rangle = \ldots$$
$$\ldots = \langle 0, 0, 1, -1, 0, 0, 0, 0, 0, 0, 0, 0, 0 \rangle$$

and the resulting unit vector $\mathbf{u}$ of this particular vector $\mathbf{a}$ would appear as

$$\mathbf{u} = \left\langle \frac{\delta S_{\mathbf{A}}}{\|\mathbf{a}\|_2}, \frac{\delta\eta_{\mathbf{A}}}{\|\mathbf{a}\|_2}, \frac{\delta I}{\|\mathbf{a}\|_2}, \frac{\delta S_{\mathbf{Y}}}{\|\mathbf{a}\|_2}, \frac{\delta\eta_{\mathbf{Y}}}{\|\mathbf{a}\|_2}, \frac{\delta\gamma_1}{\|\mathbf{a}\|_2}, \frac{\delta\gamma_2}{\|\mathbf{a}\|_2}, \frac{\delta\gamma_3}{\|\mathbf{a}\|_2}, \frac{\delta\gamma_4}{\|\mathbf{a}\|_2}, \frac{\delta B_1}{\|\mathbf{a}\|_2}, \frac{\delta B_2}{\|\mathbf{a}\|_2}, \frac{\delta B_3}{\|\mathbf{a}\|_2}, \frac{\delta B_4}{\|\mathbf{a}\|_2} \right\rangle = \ldots$$
$$\ldots = \langle 0, 0, 0.71, -0.71, 0, 0, 0, 0, 0, 0, 0, 0, 0 \rangle.$$

Thus, the directional derivative for scenario 3 is computed as

$$D_{\mathbf{u}}\lambda_1 = \nabla_s \lambda_1 \cdot \mathbf{u} = \langle 0.93, 0.88, 1.05, 0.26, 0.19, 0.02, 0.02, 0.02, 0.10, 0.01, 0.02, 0.02, 0.09 \rangle \bullet \ldots$$
$$\ldots \langle 0, 0, 0.71, -0.71, 0, 0, 0, 0, 0, 0, 0, 0, 0 \rangle = 0.56.$$

Table 2 contains the directional derivatives for each management scenario.

Consideration of the influence of multiple, simultaneous perturbations to vital rates can lead to interesting conclusions, especially if positive and negative perturbations are evaluated. Take for instance scenarios 3 and 4. Each represents a reduction in a survival rate and subsequent increase in immigration rate. Calculation of the directional derivative indicates that the two scenarios may have similar effects on λ_1 to varying degrees. Both scenarios are consistent in that they would result in a positive influence on λ_1, despite the reduction in a survival rate which was intended to reduce the population growth rate. Yet, scenario 3 would have a larger influence on λ_1 than scenario 4. In fact, the influence of scenario 4 is minimal when compared to all other perturbations.

Directional derivatives allow a formal, mathematical framework for evaluating the effects of different perturbation scenarios. This multivariate framework may reveal patterns not previously considered. Scenario 4 for example allowed for direct evaluation of an increase in one rate and decrease in another. This scenario also suggests that the overall influence on λ_1 would be minimal; however, if one only considered how a decrease in adult survival would impact λ_1 (as is represented in scenario 1 - the traditional sensitivity measurements) you might expect a greater influence on λ_1.

Scenario 5 represents the set of perturbations that would lead to the largest increase and decrease in λ_1 (i.e., perturbations in proportion to the gradient vector). While it is unlikely that this set of perturbations would occur, it does provide a benchmark to compare the results of other management scenarios. For instance, scenario 2 indicates that decreased breeding success and yearling survival will have a small influence on λ_1 when compared to the potential for change in λ_1 as represented by perturbations in scenario 5. Traditional sensitivity analyses only allow the relative ranking of single perturbations. Perturbations in proportion to the gradient vector allow for identification of an upper bound of influence on λ_1, and thus other sets of perturbations can be compared to the greatest potential influence on λ_1. This would also hold if one were using elasticities in the gradient vector.

It should be noted that the set of perturbations used in scenarios 1-4 represent unit changes, where entries of $\mathbf{u}$ were of equal magnitude. This was done because frequently it is not known that a management action will influence vital rate a_{ij} by x% but the perturbation will only influence vital rate a_{kl} by 75% of the result on x. The assumption of unit perturbations is similar to that made in traditional sensitivity analyses.

Our analytical framework for examining multivariate perturbations will allow scientists to consider and compare more realistic hypotheses concerning change in population-level vital rates, which could not be considered within the traditional perturbation analysis framework (i.e., sensitivities and elasticities). I hope that population ecology will benefit greatly from this new approach to demographic perturbation analysis.

The gradient vector and interspecific life history analyses

One of the appealing attributes of matrix population models is the ability of researchers to develop inference within applied and evolutionary arenas. Similar to statements made in the applied, intraspecific analysis, the evolutionary interpretation of matrix population models has by and large been restricted to the evaluation of individual sensitivity measurements (Caswell 2001). Consideration of the overall selection on the demography of a life history has not been presented explicitly; however, Lande (1982) provides the theoretical foundation for such an approach. The gradient vector and the maximized directional derivative overcome this deficiency.

In the following example, I selected 6 vertebrate species that span different ages of maturity (2-14 years), and I evaluate the interspecific patterns of their respective gradient vectors within the demographic landscape. Further, I compute and draw inference from a set of gradient vectors per life history composed of first- and then second-derivatives to form the set (for notation see section on Directional Derivatives and the Gradient Vector). To reiterate the distinction, a gradient vector composed of first-derivatives will be denoted as $\nabla_s \lambda_1$, and a gradient vector composed of second derivatives will be indicated as $\nabla_s^2 \lambda_1$. Within a population dynamics framework, I interpret a gradient vector composed of first-derivatives to indicate the direction of natural selection (i.e., vital rate perturbations) that will lead to the greatest increase in λ_1. Mathematically, the direction of a gradient vector composed of second-derivatives, indicates the direction of movement that will result in the greatest change in the local slope on the demographic landscape, which corresponds to shape or selection on the variance of a particular vital rate (Caswell 1996)

So that life histories presented in the interspecific example are directly comparable, I first present a simple two stage matrix model capable of describing a vast array of vertebrate life histories. Mills et al. (1999) and Neubert and Caswell (2000) independently presented a two-stage matrix population model (hereafter referred to as the MNC model) that was capable of describing a majority of vertebrate life histories with the following assumptions: individuals are censused immediately prior to the breeding season (hence a pre-breeding matrix model), the model describes an annual time step, individuals can be classified as either pre-breeders or breeders, the survival rate of pre-breeders (σ_1) and breeders (σ_2) is constant within each stage, transition from the pre-breeding to breeding stage occurs prior to the start of the breeding season, maturation rate can be described by a constant rate (γ), and fertility (ϕ) describes fecundity of breeders decremented by survival through the first year of life. The maturation rate is derived as a weighted value taking into consideration age at maturity, prebreeding survivorship, and the age distribution prior to sexual maturity for a particular life history (Caswell 2001:161). Given these assumptions, the annual MNC model takes the following form:

$$\mathbf{A} = \begin{pmatrix} \sigma_1(1-\gamma) & \phi \\ \sigma_1\gamma & \sigma_2 \end{pmatrix}.$$

The MNC model has some appealing attributes for investigations of patterns in life histories and population dynamics (Mills et al. 1999, Neubert and Caswell 2000). First, age at maturity has long been considered an important life history variable (Cole 1954, Williams 1966) with important implications for individual fitness (McGraw and Caswell 1996, Oli et al. 2002). Matrix models exist that allow incorporation of this parameter into the matrix (i.e., partial life cycles; Cole 1954, Levin et al. 1996, Oli 2003); however, the dimension of these partial life cycles is uniquely determined by the age at maturity, thereby making interspecific comparisons difficult. Second, because many of the assumptions of the MNC model are plausible (Mills et al. 1999, Neubert and Caswell 2000), use of an identical matrix across a spectrum of life histories allows for straight forward comparison of matrix properties (e.g., sensitivity structure, stable age/stage distribution, etc.). Although simplifying assumptions must be made, the MNC model is an attractive choice for interspecific life history analysis for these reasons and validates the development of a simplified demographic landscape from its structure.

Sufficient demographic data were collected from the published literature to allow parameterization of a MNC model for each respective life history (Table 3). Because I sought to explore the evolutionary interpretations of gradient vectors and directional derivatives within a demographic landscape, I chose life histories where the published demographic data yielded a λ_1 near 1.0 (Charlesworth 1980). I computed 2 gradient vectors for each life history. The first gradient vector, $\nabla_S \lambda_1$, was composed of first partial derivatives $\left(i.e., \nabla_S \lambda_1 = \left\langle \frac{\partial \lambda_1}{\partial \sigma_1}, \frac{\partial \lambda_1}{\partial \sigma_2}, \frac{\partial \lambda_1}{\partial \phi}, \frac{\partial \lambda_1}{\partial \gamma} \right\rangle \right)$ and is identical to the gradient vector used in the applied, intraspecific example. From a mathematical perspective, movement on the demographic landscape in the direction of $\nabla_S \lambda_1$ will result in the maximization of the directional derivative, and thus the set of vital rate perturbations that will have the greatest influence on λ_1. From an evolutionary perspective, perturbation of vital rates in proportion to $\nabla_S \lambda_1$ will result in the selection gradient where directional selection is maximized (Lande 1982, Caswell 1996, 2001, Rice 2002). Directional selection will most influence the mean value of a trait (Rice 2004).

The second gradient vector I computed for each life history, $\nabla_s^2\lambda_1$, is one composed of second partial derivatives $\left(i.e., \nabla_s^2\lambda_1 = \left\langle \frac{\partial^2\lambda_1}{\partial\sigma_1^2}, \frac{\partial^2\lambda_1}{\partial\sigma_2^2}, \frac{\partial^2\lambda_1}{\partial\phi^2}, \frac{\partial^2\lambda_1}{\partial\gamma^2} \right\rangle \right)$ and mathematically gives the direction to move on the demographic landscape where the slope changes most rapidly. The evolutionary interpretation of this vector is the direction where nonlinear forms of selection are maximized (Lande 1982, Caswell 1996, Rice 2002). Nonlinear forms of selection will result in either stabilizing or disruptive selection which either decreases or increases the variance of a trait, respectively.

Note that $\nabla_s^2\lambda_1$ only evaluates the change in variance of a vital rate for a given movement on the demographic landscape, and does not estimate how covariance in sensitivities may influence potential variation of a vital rate. This is a major qualitative and quantitative departure between this methodology and that of Lande and Arnold (1983) and Rice (2002). The use of $\nabla_s^2\lambda_1$ assumes that selection on the variance of a particular vital rate is most influenced by the value of the rate itself, rather than covariance with another rate. Whether this assumption is a debilitating flaw in our evolutionary interpretation of the gradient vector will likely depend on the nature of the life histories under investigation; however, in this presentation to be able to directly compare both types of selection I did not consider covariance in nonlinear selection on vital rates. This is a potentially fruitful area of future research both to answer evolutionary as well as applied population dynamical questions.

I also computed the maximized directional derivative for movement in the direction of each of the gradient vectors. The evolutionary interpretation of a single directional derivative is ambiguous when one considers multiple, simultaneous selection pressures primarily due to the different scales on which fecundity and survival are measured (Morris and Doak 2004). In traditional sensitivity analysis, the sensitivity value for element a_{ij} in matrix $\mathbf{A}$ reveals the selection on that individual rate (not considering the potential selection due to covariance amongst the other vital rates in matrix $\mathbf{A}$; van Tienderen 1995). In our example the directional derivative represents the collection of selection pressures on all vital rates within a particular life history. Because of this attribute, interpretation of directional derivatives in an evolutionary context makes most sense in a comparative framework. That is, interpretation of a maximized directional derivative, either with respect to movement in the direction of $\nabla_s \lambda_1$ or $\nabla_s^2 \lambda_1$, should be interpreted in reference to maximized directional derivatives for other life histories. For example, Table 4 gives the $\nabla_s \lambda_1$ and $\nabla_s^2 \lambda_1$ vectors for each life history, as well as the maximized directional derivative for movement in the direction of $\nabla_s \lambda_1$ and $\nabla_s^2 \lambda_1$. In our selected life histories, the overall selection pressure on a life history increased with age at maturity. Whether this represents a greater influence of natural selection on life histories with later ages at maturity is debatable. The demographic landscape of the MNC model is reflective of an annual time step. How would the strength of selection, as conveyed by the maximized directional derivative, vary across life histories if the gradient vector were composed from a matrix model that represented a time step equivalent to the generation length of a particular life history? For now, it appears that life histories with greater ages of maturity have the potential to respond more quickly than life histories with short ages at maturity to equivalent levels of natural selection. A greater understanding of this point will be had when the evolutionary implications of evaluation at certain temporal scales is better understood (Horvitz and Schemske 1995).

The use of linear and nonlinear selection gradient vectors within the demographic landscape also allows for the comparison of both forms of natural selection. For example, I are able to evaluate whether certain perturbations to vital rates will have similar influence on the mean and variance of a vital rate across a range of life histories. To accomplish this I computed an angle, θ, between $\nabla_s \lambda_1$ and $\nabla_s^2 \lambda_1$ for each life history (Table 4). Larger θ values indicate that selection on the mean and variance of a vital rate are diverging. In our set of life histories I see that indeed divergence between selection on the mean and variance of a vital rate increases with age at maturity. This concept of increasing divergence between linear and nonlinear selection pressures with age at maturity can be better interpreted if one considers the selection on vital rate variance across a range of life histories. Pfister (1998) suggested that vital rates with large sensitivities should be under selection such that variance in that vital rate is reduced, as compared to vital rates with less selection pressure. Morris and Doak (2004) however demonstrated that Pfister's (1998) analysis did not completely address the question because of spurious negative correlations due to the bounding of variances in survival rates. Still, the qualitative basis for Pfister's (1998) hypothesis remains. These results suggest that selection on the variance of vital rates may not be consistent across a range of life histories. Clearly, the complete understanding of gradient vectors remains to be developed. This mathematical framework does though represent a move towards developing a greater and more holistic understanding of evolution of life histories and population dynamics itself (Turchin 2003).

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Table 1. Mean vital rates from 1973-1990 for the lesser snow goose breeding colony at La Pérouse Bay, Canada, and the sensitivity of asymptotic population growth rate, λ_1, to changes in each vital rate. Parameter values are taken from Cooch et al. (2001).

Vital rate	Mean value	$\frac{\partial \lambda_1}{\partial a_{ij}}$	Vital rate	Mean value	$\frac{\partial \lambda_1}{\partial a_{ij}}$
Adult survival ($S_{\mathbf{A}}$)	0.83	0.93	Breeding propensity, age 4 (γ_4)	0.73	0.02
Yearling survival ($S_{\mathbf{Y}}$)	0.48	0.26	Breeding propensity, age 5 (γ_5)	0.85	0.10
Adult fidelity rate ($\eta_{\mathbf{A}}$)	0.88	0.88	Breeding success, age 2 (B_2)	0.69	0.01
Yearling fidelity rate ($\eta_{\mathbf{Y}}$)	0.66	0.19	Breeding success, age 3 (B_3)	0.79	0.02
Immigration rate (I)	0.09	1.05	Breeding success, age 4 (B_4)	1.01	0.02
Breeding propensity, age 2 (γ_2)	0.31	0.02	Breeding success, age 5 (B_5)	0.95	0.09
Breeding propensity, age 3 (γ_3)	0.61	0.02			

Table 2. Results of several hypothetical management scenarios intended to reduce the asymptotic population growth rate, λ_1, for the La Pérouse Bay population of lesser snow geese. Each management scenario is composed of one, or a set of vital rates to be perturbed. The directional derivative, $D_{\mathbf{u}}\lambda_1$, represents the positive or negative influence on λ_1 for particular sets of vital rate perturbations. Management scenario 1 represents traditional sensitivity analyses where change in a vital rate is considered when all others are held constant. Management scenario 5 represents perturbation of vital rates in proportion to the gradient vector and are the set of perturbations that maximize or minimize λ_1.

Management scenario	Vital rate(s) to be perturbed	$D_{\mathbf{u}}\lambda_1$ [1]
1	$+S_{\mathbf{A}}$	0.93
	$(-S_{\mathbf{A}})$ [2]	(-0.93) [2]
1	$+\eta_{\mathbf{A}}$	0.88
	$(-\eta_{\mathbf{A}})$	(-0.88)
1	$+I$	1.05
	$(-I)$	(-1.05)
1	$+S_{\mathbf{Y}}$	0.26
	$(-S_{\mathbf{Y}})$	(-0.26)
1	$+\eta_{\mathbf{Y}}$	0.19
	$(-\eta_{\mathbf{Y}})$	(-0.19)
1	$+\gamma_2$	0.02
	$(-\gamma_2)$	(-0.02)

1	$+\gamma_3$ $(-\gamma_3)$	0.02 (-0.02)
1	$+\gamma_4$ $(-\gamma_4)$	0.02 (-0.02)
1	$+\gamma_5$ $(-\gamma_5)$	0.10 (-0.10)
1	$+B_2$ $(-B_2)$	0.01 (-0.01)
1	$+B_3$ $(-B_3)$	0.02 (-0.02)
1	$+B_4$ $(-B_4)$	0.02 (-0.02)
1	$+B_5$ $(-B_5)$	0.09 (-0.09)
2	$-B_2, -B_3, -B_4, -B_5, -S_{\mathbf{Y}}$	-0.18
3	$-S_{\mathbf{Y}}, +I$	0.56
4	$-S_{\mathbf{A}}, +I$	0.09
5	$+S_{\mathbf{A}}, +\eta_{\mathbf{A}}, +I, +S_{\mathbf{Y}}, +\eta_{\mathbf{Y}}, +\gamma_i, +B_i$	1.69
5	$-S_{\mathbf{A}}, -\eta_{\mathbf{A}}, -I, -S_{\mathbf{Y}}, -\eta_{\mathbf{Y}}, -\gamma_i, -B_i$	-1.69

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[1] $D_{\mathbf{u}}\lambda_1 = \nabla_s \lambda_1 \bullet \mathbf{u}$ where

$$\mathbf{u} = \left\langle \frac{\delta S_{\mathbf{A}}}{\|\mathbf{a}\|_2}, \frac{\delta \eta_{\mathbf{A}}}{\|\mathbf{a}\|_2}, \frac{\delta I}{\|\mathbf{a}\|_2}, \frac{\delta S_{\mathbf{Y}}}{\|\mathbf{a}\|_2}, \frac{\delta \eta_{\mathbf{Y}}}{\|\mathbf{a}\|_2}, \frac{\delta \gamma_1}{\|\mathbf{a}\|_2}, \frac{\delta \gamma_2}{\|\mathbf{a}\|_2}, \frac{\delta \gamma_3}{\|\mathbf{a}\|_2}, \frac{\delta \gamma_4}{\|\mathbf{a}\|_2}, \frac{\delta B_1}{\|\mathbf{a}\|_2}, \frac{\delta B_2}{\|\mathbf{a}\|_2}, \frac{\delta B_3}{\|\mathbf{a}\|_2}, \frac{\delta B_4}{\|\mathbf{a}\|_2} \right\rangle \text{ and}$$

$\mathbf{a} = \langle \delta S_{\mathbf{A}}, \delta \eta_{\mathbf{A}}, \delta I, \delta S_{\mathbf{Y}}, \delta \eta_{\mathbf{Y}}, \delta \gamma_2, \delta \gamma_3, \delta \gamma_4, \delta \gamma_5, \delta B_2, \delta B_3, \delta B_4, \delta B_5 \rangle$. The vector $\mathbf{a}$ represents a vector of actual perturbations to vital rates, and $\|\mathbf{a}\|_2$ is the length of vector $\mathbf{a}$. $D_{\mathbf{u}}\lambda_1$ is the value from the dot product of $\nabla_s \lambda_1$ and unit vector $\mathbf{u}$.

[2] Represents the results of positive (e.g., $+S_{\mathbf{A}}$) or negative (e.g., $-S_{\mathbf{A}}$) perturbations to a single vital rate.

Table 3. Vital rate values and age at maturity for several vertebrate species modeled with the MNC matrix population model. See *Gradient vector and interspecific life history analyses* section for description of MNC model.

		Parameter values				
Species	Age at maturity (years)	σ_1[6]	σ_2[7]	ϕ[8]	γ[9]	λ_1[10]
Caribou[1] (*Rangifer tarandus*)	2	0.71	0.93	0.30	0.42	1.07
Red deer[2] (*Cervus elaphus*)	3	0.93	0.91	0.20	0.31	1.05
Atlantic puffin[3] (*Fratercula arctica*)	5	0.78	0.94	0.32	0.11	1.03
Painted turtle[4] (*Chrysemys picta*)	7	0.76	0.76	1.88	0.05	1.02
Wandering albatross[3] (*Diomedea exulans*)	10	0.86	0.93	0.21	0.05	0.98
Desert tortoise[5] (*Gopheus agassizii*)	14	0.81	0.94	1.88	0.01	1.03

Data sources: [1]Messier et al. (1988); [2]Benton et al. (1995), Albon et al. (2000); [3]Sæther and Bakke 2000; [4]Heppell (1998); [5]Heppell (1998).

[6]Annual survival of individuals prior to attainment of sexual maturity; [7]Annual survival of individuals after attainment of sexual maturity; [8]Annual fertility of sexually mature individuals; [9]Annual maturation rate of individuals from pre-sexually mature status to sexually mature status. Maturation rate was calculated as a weighted average of the stable age distribution within the pre-breeding stage (Caswell 2001:161); [10]Asymptotic population growth rate of MNC model.

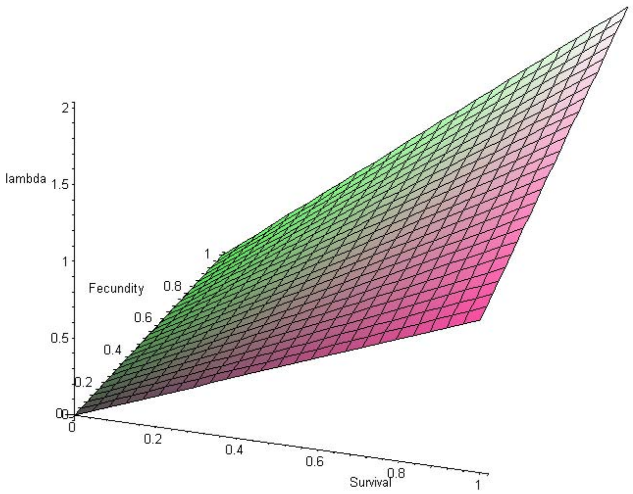
Table 4. Gradient vectors representing linear ($\nabla_s \lambda_1$) and nonlinear ($\nabla_s^2 \lambda_1$) selection pressures on several vertebrate species modeled with the MNC matrix model. Linear selection on a life history is approximated with the gradient vector composed of first partial derivatives whereas nonlinear selection is assessed with a gradient vector composed of second partial derivatives. The directional derivatives for each gradient vector represent the maximized directional derivative which is movement on the demographic landscape in the direction of the gradient vector. The angle between the linear selection gradient vector and the nonlinear selection gradient vector per life history represents the similarity of selection pressures to simultaneously influence mean values and variance for demographic traits. As θ increases, selection pressures will have less of a collective influence on both the mean value and variance of a vital rate.

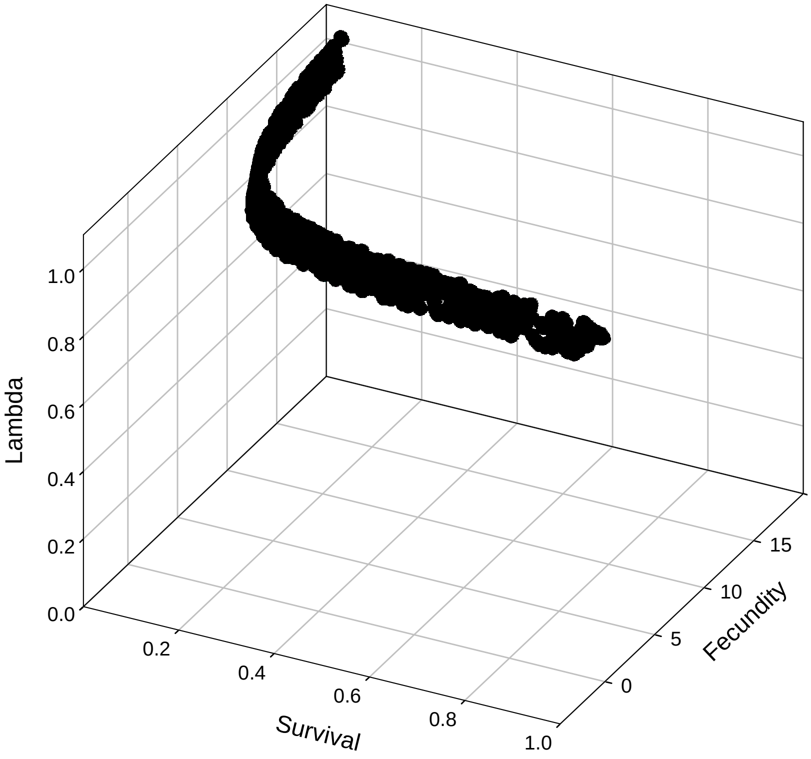
Species	$\nabla_s \lambda_1 = \left\langle \frac{\partial \lambda_1}{\partial \sigma_1}, \frac{\partial \lambda_1}{\partial \sigma_2}, \frac{\partial \lambda_1}{\partial \phi}, \frac{\partial \lambda_1}{\partial \gamma} \right\rangle$	$D_{\mathbf{u}} \lambda_1$	$\nabla_s^2 \lambda_1 = \left\langle \frac{\partial^2 \lambda_1}{\partial^2 \sigma_1}, \frac{\partial^2 \lambda_1}{\partial^2 \sigma_2}, \frac{\partial^2 \lambda_1}{\partial^2 \phi}, \frac{\partial^2 \lambda_1}{\partial^2 \gamma} \right\rangle$	$D^2{}_{\mathbf{u}} \lambda_1$	θ[1]
Caribou (*Rangifer tarandus*)	$\langle 0.26, 0.82, 0.38, 0.15 \rangle$	0.95	$\langle 0.21, 0.36, -0.36, -0.31 \rangle$	0.63	1.29
Red deer (*Cervus elaphus*)	$\langle 0.29, 0.75, 0.53, 0.10 \rangle$	0.96	$\langle 0.42, 0.69, -1.00, -0.38 \rangle$	1.35	1.52
Atlantic puffin (*Fratercula arctica*)	$\langle 0.27, 0.80, 0.21, 0.44 \rangle$	0.97	$\langle 0.80, 0.77, -0.20, -2.45 \rangle$	2.70	1.68
Painted turtle (*Chrysemys picta*)	$\langle 0.62, 0.54, 0.07, 2.21 \rangle$	2.35	$\langle 0.75, 0.91, -0.02, -24.78 \rangle$	24.80	2.74
Wandering albatross (*Diomedea exulans*)	$\langle 0.28, 0.75, 0.19, 0.64 \rangle$	1.05	$\langle 1.71, 1.70, -0.37, -8.95 \rangle$	9.28	2.00
Desert tortoise (*Gopheus agassizii*)	$\langle 0.36, 0.72, 0.03, 4.65 \rangle$	4.72	$\langle 1.46, 1.26, -0.004, -168.24 \rangle$	168.25	2.96

[1] The angle between the vector $\nabla_s \lambda_1$ and $\nabla_s^2 \lambda_1$ given as $\theta = \cos^{-1}\left(\frac{\nabla_s \lambda_1 \bullet \nabla_s^2 \lambda_1}{\left|\nabla_s \lambda_1\right| \left|\nabla_s^2 \lambda_1\right|} \right)$

Figure 1. Theoretical representation of the demographic landscape for the population model $\lambda = S(1+F)$ where λ is the annual population growth rate, S is the annual survival rate of individuals in the population, and F is fecundity (i.e., birth rate). Although this population model does not reflect age structure (as do matrix population models), this simplified population model is illustrative of a visual representation of a demographic landscape. Demographic landscapes of matrix population models are conceptually similar to the one presented here, yet are not easily visualized since they exist as a surface in hyperspace.

Note: This figure is still a work in progress. The ultimate figure 1 will be a surface as in the first graph below, but will be bounded to the region represented in the bottom graph. The points in the bottom graph are simulated data of combination of S and F that produce 0.95$\leq$ *Lambda* $\leq$ *1.05. Also, points P1 and P2 referred to in text still need to be included, but their placement can easily be visualized on these 2 graphs.*


lambda
2
1.5
1
0.5
0
Fecundity
0.2
0.4
0.6
0.8
1
Survival
0
0.2
0.4
0.6
0.8
1


Lambda
1.0
0.8
0.6
0.4
0.2
0.0
Survival
0.2
0.4
0.6
0.8
1.0
Fecundity
0
5
10
15