MULTIVARIATE PERSPECTIVES ON PATCH USE BY MASKED BOBWHITES

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Abstract: Models that discriminate habitat patches acceptable to wildlife assist biologists in managing habitat, evaluating the effects of management treatments, and selecting areas for development or preservation. We used neural network modeling to discriminate between used and random patches for the endangered masked bobwhite (*Colinus virginianus ridgwayi*) in Sonora, Mexico, and Arizona during 1994–96. Input variables, thought to encompass the habitat space of bobwhites, were canopy coverage of woody vegetation (%), exposure of bare ground (%), exposure to ground predators (m^2), exposure to aerial predators (m^3), and operative temperature (°C). A neural model developed with data from Mexico correctly classified 87.4% of patches for training (n = 483) and validation data (n = 118). The model developed for Arizona correctly classified 82.3% of patches for training data (n = 265) and 78.1% for validation data (n = 64). Mathematical transplants of Mexico bobwhites to Arizona habitat and of Arizona bobwhites to Mexico habitat revealed that bobwhites from Mexico (native) were adapted to a broader range of conditions than those in Arizona (reintroduced). For masked bobwhites and probably other species, the contingent nature of habitat features in a multivariate sense may permit the redress of a habitat deficiency without addressing the perceived deficiency per se.

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The masked bobwhite occurs as remnant populations on Buenos Aires National Wildlife Refuge, Arizona, and on a few private ranches in Sonora, Mexico (U.S. Fish and Wildlife Service 1995). The populations in Mexico consist of native birds, whereas those in Arizona represent birds propagated and released on the refuge and wild progeny of released birds. The birds released in Arizona arose from founders captured in Mexico in 1964 (Carpenter et al. 1991) and held in propagation facilities. More than 20,000 offspring from these founders have been released on the refuge since 1985; reproduction in the wild has been observed (U.S. Fish and Wildlife Service 1995).

Habitat in the areas occupied by masked bobwhites changes with weather trends, human activities, and ecological processes. To preserve the masked bobwhite and foster its increase in light of these changes, it is necessary to have a quantitative idea of properties of habitat to which this bird is adapted. This knowledge assists management biologists in prescribing management practices that will create acceptable habitat. The knowledge also permits the evaluation of habitat treatments and trends without having to directly measure individual bird response, which is difficult for endangered species. A quantitative understanding of habitat properties important to a species aids in identifying priority areas for preservation or development.

We previously reported on the habitat relations of masked bobwhites from a univariate perspective (Guthery et al. 2000). This analysis

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provided basic information on statistical properties of habitat and preference-avoidance relations. Our previous paper did not address how habitat and thermal conditions might or might not interact in a multivariate sense to influence patch-use decisions. To the extent that multiple factors govern patch use, knowledge of the interrelations among factors is necessary for understanding behavior in the field and for developing sound management plans.

Accordingly, our present purpose was to develop and test multivariate patch discrimination models for masked bobwhites in Sonora and Arizona. We measured habitat properties at used and random patches and then developed neural discrimination models from these data. We then modeled habitat features with the neural models to understand how patch discrimination (used, random) varied with a particular habitat feature, and to explore how habitat features interacted in multidimensional habitat space. Models developed from Sonora and Arizona data allowed us to perform mathematical transplants of Mexico bobwhites to Arizona habitat, and of Arizona bobwhites to Mexico habitat. These "transplants" provided insight on the comparative performance of native and reintroduced populations. Finally, our results provided insights concerning the theory of habitat in wildlife management; we discuss these insights.

STUDY AREAS AND METHODS

Detailed information on study areas and field methodology is available in Kopp et al. (1998), Forrester et al. (1998), and Guthery et al. (2000); we present a brief overview of that information to orient the reader. Study areas in Sonora and Arizona were characterized by semiarid environments (37–40 cm of annual precipitation) supporting rangeland vegetation with variable amounts of woody cover. Sampling in Sonora took place on a 32,000-ha private cattle ranch. Buenos Aires National Wildlife Refuge (48,000 ha) was the study area in southern Arizona.

We measured habitat properties at organism-centered and randomly located patches (Brennan et al. 1986) following Kopp et al. (1998). Sampling took place during June 1994–November 1995 in Sonora and during October 1994–September 1996 in Arizona. The data relate to points where bobwhites were first observed (flushing points).

We developed neural discrimination models based on 4 habitat variables and 1 microclimate variable measured at each used (organism-centered) and random patch. The habitat variables included mean canopy coverage of woody vegetation (%, Canfield 1941), mean exposure of bare ground (%, Daubenmire 1959), exposure to terrestrial predators (disc of vulnerability, m^2, Kopp et al. 1998), exposure to aerial predators (cone of vulnerability, m^3, Kopp et al. 1998:Fig. 1), and operative temperature (Forrester et al. 1998). These variables were thought to explicitly or implicitly capture the key structural properties of the habitat space of bobwhites based on species-habitat models (Schroeder 1985, Bidwell et al. 1991, Rice et al. 1993) and preference-avoidance models (Kopp et al. 1998, Guthery et al. 2000). The habitat variables related to food-finding, predator avoidance, and heat avoidance. Heat avoidance may explain the field behavior of bobwhites as well as predator avoidance (Forrester et al. 1998), which justifies our inclusion of operative temperature. Our definition of a patch is a small but variable-sized area that governs adaptive habitat use decisions in the near term.

We used neural network modeling with backpropagation of errors (Kosko 1992, Hagan et al. 1996, Smith 1996) to discriminate on a multivariate basis between used and random patches. Backpropagation modeling is a nonparametric technique whereby the form of a relationship is determined by the data rather than by the tool used to analyze the data (Smith 1996). Multicollinearity of independent variables does not invalidate neural modeling. We used a 5–10–2 neural model (5 input nodes, 10 hidden nodes, 2 output nodes). Input (independent variables) consisted of the 4 habitat variables and 1 microclimate variable defined above. Output consisted of a classification score (0.8 if true, 0.2 if false) for used and random patches. We interpreted scores >0.5 to predict used and scores <0.5 to predict random patches.

About 20% of the data from each state (Sonora and Arizona) were reserved for validating models and the remainder were used in training the models with data specific for each state. Training involves the adjustment of weights and biases (parameters) connecting nodes to minimize the mean squared error associated with observed and predicted values. The models converged to minimal errors within 2,500–3,500 iterations. We used commercially available software (California Scientific Software, Nevada

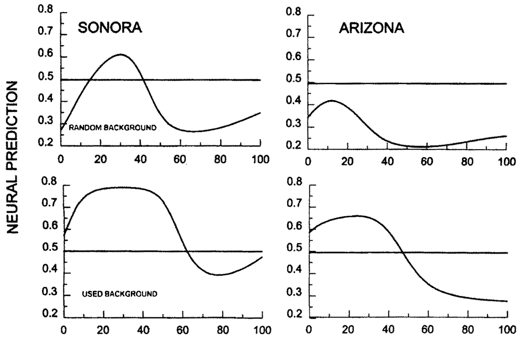

Fig. 1. Neural classifications of habitat patches for masked bobwhites in Sonora and Arizona based on canopy coverage of woody vegetation, 1994–96. The top figures show classifications with 4 input nodes held constant at mean values in the random environment; constants were mean values at patches used by masked bobwhites in the bottom figure.

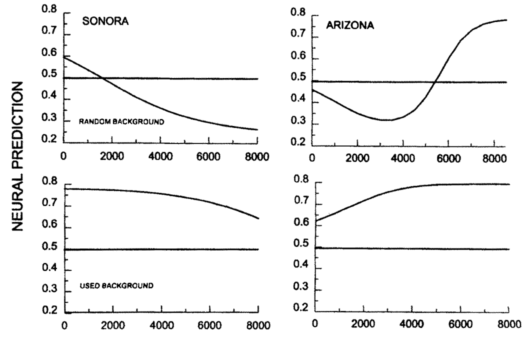

Fig. 2. Neural classifications of habitat patches for masked bobwhites in Sonora and Arizona based on the disc of vulnerability (exposure to ground predators), 1994–96. The top figures show classifications with 4 input nodes held constant at mean values in the random environment; constants were mean values at patches used by masked bobwhites in the bottom figure.

City, California, USA). We present the predictions of backpropagation models for a single variable with other variables held constant at mean values from random patches (random-mean background) and at mean values from used patches (used-mean background). See Guthery et al. (2000:Table 1) for values of the means used in modeling and for estimated probability distributions associated with these means. These backgrounds, though arbitrary, were considered meaningful from a biological (used mean) or management (random mean) standpoint. The backgrounds were necessary to provide graphical images of a 5-dimensional response surface; i.e., images cannot be developed for >3 dimensions.

RESULTS

Discrimination of Patches

A backpropagation model constructed with data (n = 483) from Sonora correctly classified 95.9% of used patches and 73.9% of random patches; the correct classification rate, overall, was 87.4%. The Sonora model correctly classified 94.5% of used patches and 75.6% of random patches with a data set for validation (n = 118), giving an overall correct classification rate of 87.4%. A model constructed with data from Arizona (n = 265) correctly classified 75.2% of used patches and 87.2% of random patches for an overall rate of 82.3%. The model correctly classified 78.1% of observations on validation data (n = 64), including 88.9% correct classifications for used patches and 70.3% correct for random patches.

Under a random-mean background, the Sonora model classified patches as used if canopy coverage of woody vegetation ranged between about 15 and 40% (Fig. 1). Patches were classified as used under a broader range (0–60%) under the used-mean background. The Arizona model suggested classification was independent of woody cover under the random-mean background. In other words, under the random-mean background, increases in woody cover were not associated with increases in classifications of used patches (all patches were classified as random). Under the used mean background, however, patches were classified as used if canopy coverage of woody vegetation ranged between 0 and 45%. Models from Sonora and Arizona indicated that as habitat features other than canopy coverage of woody vegetation trended from mean values at used patches to mean values at random patches, the range of values for woody cover leading to classifications of use constricted.

In Sonora, discs of vulnerability <1,800 m^2 resulted in classifications of used patches under the random-mean background, whereas classification was nonresponsive to the disc under the used-mean background (Fig. 2). Thus, smaller discs increased patch usability if other habitat features were less than optimum, whereas variation in disc size had no effect if other habitat features were acceptable. Classifications for the random-mean background were nonsensical for the Arizona model; i.e., the model classified patches as used if exposure to terrestrial pred-

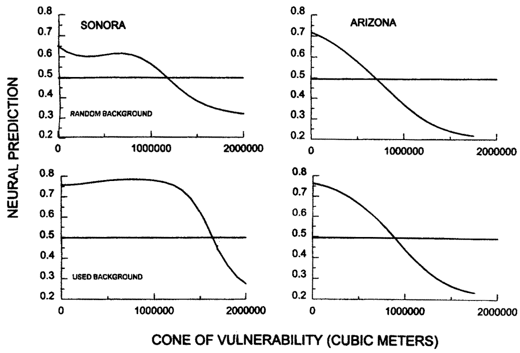

Fig. 3. Neural classifications of habitat patches for masked bobwhites in Sonora and Arizona based on the cone of vulnerability (exposure to aerial predators), 1994–96. The top figures show classifications with 4 input nodes held constant at mean values in the random environment; constants were mean values at patches used by masked bobwhites in the bottom figure.

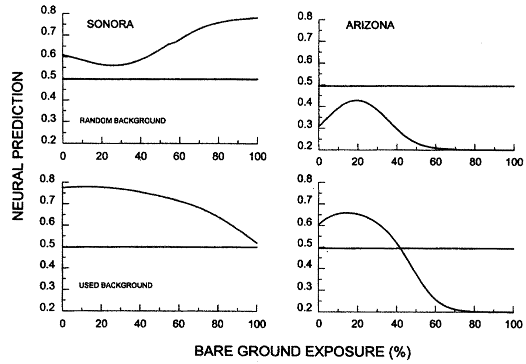

Fig. 4. Neural classifications of habitat patches for masked bobwhites in Sonora and Arizona based on exposure of bare ground, 1994–96. The top figures show classifications with 4 input nodes held constant at mean values in the random environment; constants were mean values at patches used by masked bobwhites in the bottom figure.

ators was >5,800 m^2. The classifications for the used-mean background were similar to those of the Sonora model; i.e., classification was nonresponsive to the disc with other variables set at mean values for used patches.

Classifications were sensitive to the cone of vulnerability in both Sonora and Arizona (Fig. 3). Under the random-mean background, patches were classified as used if the cone was <1,250,000 m^3 in Sonora and <750,000 m^3 in Arizona. The acceptable range for used classifications increased in Sonora to <1,600,000 m^3 and in Arizona to <900,000 m^3 under the used-mean background.

The classification of used patches was not sensitive to the exposure of bare ground under random- or used-mean backgrounds in Sonora (Fig. 4). The backpropagation model classified patches as used, regardless of bare ground exposure. In Arizona, all patches were classified as random under the random-mean background, regardless of the value of bare ground exposure. Conversely, under the used-mean background, patches were classified as used if bare ground exposure was <40%.

Operative temperature at 15 cm aboveground had variable effects on classifications in Sonora and Arizona (Fig. 5). The backpropagation model based on Sonora data classified all patches as random, regardless of operative temperature, under the random-mean background. Conversely, the model classified all patches as used, regardless of operative temperature, under the used-mean background. Patches under the random-mean background were classified as used if operative temperature was <25° C based on the Arizona model. The range expanded to <32° C under the used-mean background.

Mathematical Transplants

When the Sonora model was applied to habitat in Arizona (n = 329), which is the mathematical equivalent of transplanting wild bobwhites from Sonora to Arizona, the proportion of patches correctly classified was 0.56 ± 0.027, indicating a slight improvement on chance (0.5 as proportion correct). The Sonora model misclassified 69.9% of random patches as used patches and 7.4% of used patches as random. The backpropagation model developed from Arizona data correctly classified 0.69 ± 0.018 of

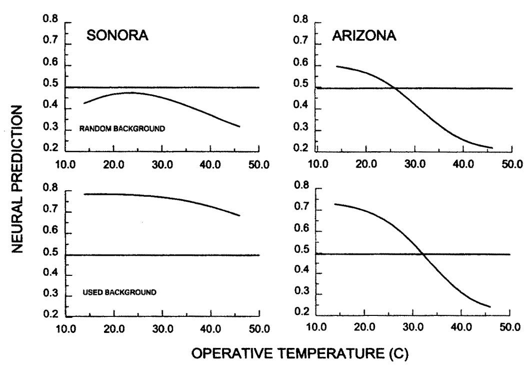

Fig. 5. Neural classifications of habitat patches for masked bobwhites in Sonora and Arizona based on operative temperature (°C) at 15 cm aboveground, 1994–96. The top figures show classifications with 4 input nodes held constant at mean values in the random environment; constants were mean values at patches used by masked bobwhites in the bottom figure.

patches in Sonora (n = 601). The model misclassified 18.0% of random patches as used and 39.1% of used patches as random. The outcome of these mathematical transplants suggests broader adaptability of masked bobwhites from Sonora (native populations) in comparison with those from Arizona (reintroduced population). That is, Sonora bobwhites apparently would find more random patches that were usable, if in Arizona, and Arizona bobwhites would find more used patches that were classified as random, if in Sonora.

DISCUSSION

Model Performance

Whereas the neural models correctly classified >78% of used and random patches with validation data, model output seemed unreliable in some situations. For example, use classifications for discs of vulnerability >5,800 m^2 under the random-mean background in Arizona (Fig. 2) were contrary to the expected behavior of bobwhites (Kopp et al. 1998, Guthery et al. 2000). We attribute this particular problem to aberrant observations (outliers) that influenced weights and biases in the neural model. Another biologically unacceptable modeling outcome was the insensitivity of bobwhites in Sonora to operative temperature under the used-mean background (Fig. 5). Texas bobwhites avoid points in space-time with operative temperatures >39° C (Forrester et al. 1998). Temperatures above this landmark result in hyperthermia. Our measurement of operative temperature at sign for some samples in Sonora (Guthery et al. 2000) may have contributed to the unreliable modeling outcomes for bobwhites in Sonora. Our inclusion of operative temperature in the discrimination model was justified, because of evidence that masked bobwhites in Sonora prefer operative temperatures <32°C (Guthery et al. 2000).

The neural models developed with data from Arizona and Sonora gave qualitatively similar results for canopy coverage of woody vegetation (Fig. 1), the disc of vulnerability under the used-mean background (Fig. 2), and the cone of vulnerability (Fig. 3). Differences in response to operative temperature (Fig. 5) probably arose because of sampling procedures, as discussed above. Exposure of bare ground was not a useful discriminator of habitat patches in Sonora, because patches were classified as used regardless of exposure (Fig. 4). Conversely, bare ground was diagnostic of bobwhite habitat in Arizona under the used-mean background. The difference between populations in response to exposure of bare ground probably was associated with differences in the general nature of the study areas. The Sonora study area was grazed and largely devoid of herbaceous cover for half of the year or more. Thus, bobwhites had little chance to exercise use-nonuse behavior with respect to bare ground. The lack of grazing on the Arizona study area resulted in more herbaceous cover and permitted bobwhites to exercise selectivity with respect to exposure of bare ground.

Behavior of Reintroduced Bobwhites

Backpropagation modeling revealed a tendency for Arizona bobwhites to be more narrowly adapted to habitat features than Sonora bobwhites. Whether the radiotransmitters attached to a portion of the masked bobwhites in Arizona (Guthery et al. 2000) affected their habitat relations is unknown. We recognize that radiotransmitters could have affected the field behavior of our sample from Arizona. However, a radiotagged individual would have to influence the behavior of an entire group for bias to occur; this seems unlikely.

Multivariate Habitat Relations

The multivariate analysis provided insights that may apply specifically in the management of masked bobwhites as well as more generally in the theory of wildlife habitat relations. We frame these arguments in terms of a univariate habitat suitability index, which describes habitat suitability (y) as a function of some habitat feature (x). Suitability indices are structural components of species-habitat models (Schroeder 1985, Rice et al. 1993). For example, habitat suitability for some species might be described as a function of the canopy coverage of woody vegetation. Our results indicated that a single habitat suitability index is unlikely to exist. Rather, the nature of a suitability index depends upon the values of all habitat features known or presumed to be relevant in the adaptive makeup of a wild animal. For example, consider the neural discrimination functions for classification of used and random habitat based on canopy coverage of woody vegetation (Fig. 1). The function described by these classification scores could be considered an approximation of a habitat suitability index. The point is that the nature (shape) of the suitability index changed with the values of other variables (used vs. random backgrounds illustrated); hence, there may be (infinitely) many suitability indices that describe the habitat relation between masked bobwhites and woody cover.

We also observed that if classifications were sensitive to one of the habitat variables examined, the range of acceptable values for a feature (classified as used point) were broader under the used-mean background than under the random-mean background. This relation held for canopy coverage of woody vegetation (Fig. 1) and the cone of vulnerability (Fig. 3). The common-sense principle emanating from this pattern is that masked bobwhites, and perhaps other species, may be less sensitive to any particular habitat feature if other habitat features are closer to acceptable levels (used-point mean versus random-point mean as constants). This outcome would be expected if wildlife responds to habitat suitability indices that are contingent upon values for other relevant habitat features.

The probable existence of contingent suitability indices for any habitat feature means that management might be able to redress a perceived or measured deficiency in 1 habitat variable by managing other variables. For example, consider a situation of 10% canopy coverage by brush in Sonora under the random-mean background (Fig. 1). Management that moved the disc and cone of vulnerability, exposure of bare ground, and operative temperature from the random- towards the used-mean background (Guthery et al. 2000:Table 1) could counteract a deficiency of woody cover without changing woody cover (Fig. 1).

Undoubtedly, our understanding of multivariate habitat relations is primitive. Whereas the relations are abstruse, they are not intractable, as our neural models demonstrated.

MANAGEMENT IMPLICATIONS

Biologists have long recognized that bobwhite populations maximally express demographic potential on an area when the area provides the opportunity for unconstrained use of space through time (Stoddard 1931, Leopold 1933, Errington and Hamerstrom 1936, Lehmann 1984). Guthery (1997) elaborated the importance of space–time maximization, and showed that a variety of patch configurations leads to space–time maximization (Guthery 1999). The discrimination models we developed and validated may be applied in the context of the space–time hypothesis.

Any area of interest may be randomly sampled in space through time for the 5 variables we used as model inputs. The quality of an area is defined as the proportion of points in space–time that provide acceptable habitat (Guthery 1997). The neural models can be used to classify sampled patches on an area of interest: the higher the proportion of patches classified as used, the better the quality of the area for bobwhites. Under space–time logic, the models can be used to evaluate the effects of habitat treatments (grazing, burning, spraying, mechanically treating) and to evaluate sites for reintroductions.

Applied ecologists need to recognize the contingent nature of formal or personal suitability models that relate the welfare of a wildlife species to a single habitat feature. There may be as many suitability models as there are sets of values for other habitat features deemed relevant. The interplay of habitat features in a multivariate sense may permit the redress of a habitat deficiency without addressing the perceived deficiency per se. This hypothesis should be tested in field experiments.

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