BIRD ABUNDANCE AS AN INDICATOR OF HABITAT QUALITY FOR BREEDING BIRDS

by

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A Thesis Submitted to the Faculty of the

SCHOOL OF RENEWABLE NATURAL RESOURCES

In Partial Fulfillment of the Requirements
For the Degree of

MASTER OF SCIENCE
WITH A MAJOR IN WILDLIFE AND FISHERIES SCIENCE

In the Graduate College

THE UNIVERSITY OF ARIZONA

1 9 9 5

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ACKNOWLEDGMENTS

I would like to acknowledge all who assisted on this project. Specifically, I would like to thank Bill Mannan for providing me the opportunity to conduct this study and for his guidance and participation throughout. I would also like to thank the other members of my committee, Bill Shaw and Bill Matter, for providing further direction for the project proposal and final manuscript, as well as for my entire degree program. Steve Rosenstock has been of tremendous assistance; establishing study plots, providing data on bird abundance, and reviewing this manuscript. The efforts of my assistants in the field have been invaluable to my research. Finally, I would like to express my appreciation for the Arizona Game and Fish Department for providing funding for this project.

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ABSTRACT

Reproductive success and survival of birds often are impractical to measure. Therefore, biologists frequently rely on measures of bird abundance alone to evaluate habitat quality for breeding birds. I examined whether results from standard survey techniques for birds during the breeding season reflected number of nesting pairs and reproductive success of 5 passerine species. Abundance of 3 species was positively associated with number of nesting pairs, but the relationship between abundance and reproductive success varied among these species. Differences in detectability of breeding males may partly explain why abundance and number of nesting pairs were related in some species and not in others. Variations in the availability and quality of habitat patches among plots could produce the different relationships I observed between abundance and reproductive success. My results suggest that measures of reproductive success as well as abundance should be used to determine habitat quality for breeding birds.

INTRODUCTION

Abundance of birds in an area often is the basis for assessing the relative quality of that area as breeding habitat for birds. High abundance of birds of a given species is generally assumed to reflect high quality breeding habitat for that species. Estimates of bird abundance are used to evaluate habitat quality among vegetation types, or before and after habitat manipulations (Mannan and Meslow 1984, Hutto 1989, and Tobalske et al. 1991). Estimates of abundance also are the foundation for most models of habitat suitability (e.g., habitat suitability index, habitat capability, and Bayesian and pattern recognition models).

Under some conditions, however, abundance alone may be a misleading indicator of habitat quality (Van Horne 1983, Vickery et al. 1992a). Standard survey techniques for birds during the breeding season may include nonbreeding as well as breeding individuals (Von Haartman 1956, Baskett et al. 1978, Wilson and Bart 1985), thus confounding assessment of habitat quality. Abundance also may indicate the response of birds to previous rather than current habitat conditions (Hilden 1965, Wiens and Rotenberry 1985). Finally, high abundance of subordinate individuals, forced out of areas providing higher or more stable levels of resources, may be observed in places where resources are insufficient for breeding (Van Horne 1983). For example, Atwood (1980) observed flocks of non-breeding Santa Cruz Island scrub jays (*Aphelocoma coerulescens*) in areas unsuitable for nesting.

Van Horne (1983) noted, over a decade ago, that the potential problems associated with using abundance alone as an indicator of habitat quality could be partly solved by developing an index of quality that incorporates measures of reproductive success and survival. Van Horne's (1983) ideas about how to measure habitat quality are generally accepted, but many efforts to evaluate habitat quality for breeding birds continue to rely primarily on bird abundance (Wiens and Rotenberry 1985, Hutto 1989, Tobalske et al. 1991) because information on reproductive success and survival often is difficult or expensive to obtain.

Because abundance of birds remains a common measure of habitat quality for breeding birds, it is important to investigate whether estimates of bird abundance are positively correlated with reproductive success. I examined whether results from standard survey techniques for birds during the breeding season accurately reflected number of nesting pairs and reproductive success of 6 species of passerine birds.

METHODS

Study Area

My study was part of a broad-scale investigation conducted by the Arizona Game and Fish Department to evaluate habitat relationships of avian species breeding in ponderosa pine (*Pinus ponderosa*) forests in northern Arizona. Sixteen plots each 400 m square (16 ha) were established in ponderosa pine stands on the Coconino National Forest and Navajo Army Depot, within 95 km of Flagstaff, Arizona (35 11'W 111 39'N). The plots ranged in elevation from 2042 to 2426 m. Each plot included 4 counting stations spaced 200 m apart and 100 m from the edges of the plot. To sample a range of bird abundance, I selected plots among stands that varied in abundance of grasses, Gambel's oak (*Quercus gambelii*) trees, young and mature pines, and snags.

Bird Abundance and Number of Nesting Pairs

I attempted to locate all nests of 6 passerine species on each plot: American robin (*Turdus migratorius*), dark-eyed junco (*Junco hyemalis*), pygmy nuthatch (*Sitta pygmaea*), solitary vireo (*Vireo solitarius*), white-breasted nuthatch (*Sitta carolinensis*), and western bluebird (*Sialia mexicana*). I chose these species because they were relatively abundant and nested in places where I could observe their behavior.

I searched for nests on 6 plots between 20 May and 6 July, 1993 and on 10 plots between 24 May and 6 July, 1994. Survey dates were selected to overlap peaks of breeding activity for songbirds in the Flagstaff area. I searched for nests on each plot for 46 observer-hours. Searches were conducted in the mornings (0500 - 1100 hrs) and early evenings (1600 - 1930 hrs) to coincide with daily peaks in bird activity. I did not search plots when winds exceeded 40 km/hr or if precipitation exceeded a light drizzle. Plots searched in 1993 were each visited 8-9 times and plots searched in 1994 were each visited 5 times. I visited each plot at least once a week.

Within each year, each of 2 to 4 observers searched for nests on all plots. Searches on a given day were conducted by 2 observers simultaneously. Observers searched opposite halves of the plot, then switched places with the other observer midway through the search period. Plot halves were flagged every 50 m on the periphery to delineate the boundaries of each observer's search area and to provide reference points. Observers searched each half systematically by starting at one corner of the plot, then walking slowly along a series of parallel lines with endpoints marked by the flagging. Observers maintained a constant pace while searching (2-3 ha/hr) so that equal time was spent in each portion of the plot.

Observers used behavioral cues exhibited by nesting birds (Martin and Guepel 1993) to facilitate locating nests. Males that did not exhibit such behavioral cues were followed no more than 15 min. Females or individuals exhibiting nesting behaviors were followed up to 30 min. Observers minimized disturbance to birds by following them from as far away as possible (minimum distance of 15 m) and leaving the area if a bird exhibited signs of distress, such as vigorous calling (Martin and Guepel 1993). Nest locations were described by taking a bearing and pacing from reference marks (counting stations and flagged trees).

Point-count surveys (Reynolds et al. 1980) were conducted independently by personnel from the Arizona Game and Fish Department (AGFD). Each plot was surveyed 3 times, with more than 1 week between surveys. Surveys were conducted between 0500 and 0830 hrs. Counts at each of 4 points lasted 8 min, with a 2-min waiting period before recording observations. Observers recorded species, age and sex (if known), number of individuals, distance from the observer, and whether the bird was singing, calling, or observed visually. Each plot was surveyed once by each of 3 observers.

I determined the number of singing males and the total of all adults detected within 100 m of each counting station on each visit from the point-count data. I summed the largest values among the 3 visits to calculate the total singing males and the total adults for each plot. I determined bird abundance for a given species and plot from the index (either singing males or all adults) that produced the highest total across plots (Reynolds et al. 1980). For pygmy nuthatches, which often nest and forage in groups, I also estimated group abundance (Buckland et al. 1993).

I tested whether results from point-counts accurately reflected number of nesting pairs by comparing the ranks of plots based on bird abundance to the ranks of plots based on number of nests for each species across all 16 plots (Spearman's rank correlation coefficient [Zar 1984]).

Bird Abundance and Reproductive Success

Limitations on sample size of nests precluded the use of Mayfield's method of estimating nest success (Mayfield 1975). Therefore, I estimated nest success by examining reproductive success of territorial males (Vickery et al. 1992b). I estimated the number of territories by mapping the location of territorial males of each species on 9 visits to each plot (International Bird Census Committee 1970). Because plots surveyed in 1994 were visited only 5 times, 2 observers independently mapped locations of territorial males on 4 of 5 visits. Nest locations were used to help identify some territories on composite maps.

I monitored reproductive success at each territory by recording observations of mated pairs and monitoring activity at nests. Ground or open-cup nests were checked directly with a mirror pole, or from a distance with binoculars. Nesting stage at cavity nests was determined by watching the cavity for 10 min and recording observations of deliveries of nesting material, or deliveries of food to incubating females or food-begging nestlings.

I assigned a rank to each territory according to the nesting stage achieved as an index of reproductive success (Vickery et al. 1992b). I did not rank territories according to presence of fledglings, as did Vickery et al. (1992a), due to the difficulty in observing when young fledged and determining to which nest fledglings belonged. I used the following criteria for each rank:

rank 0 -- Territory occupied for less than the minimum number of days required for incubating and fledging young;

rank 1 -- Territory occupied for at least the minimum number of days required for incubating and fledging young;

rank 2 -- Presence of mated pair;

rank 3 -- Nest building or incubation occurred; and

rank 4 -- Presence of nestlings.

To examine whether bird abundance reflected reproductive success for each species, I compared ranks of reproductive success among plots grouped into 3 categories of abundance based on whether the plot supported a low, medium, or high number of territorial males of a given species (Vickery et al. 1992a)(Kruskal-Wallis test [Zar 1984]). Plots with the minimum or maximum values for territory density were assigned to the low or high abundance categories respectively. Plots with median values were placed in the medium abundance category. All other plots were assigned to categories so that each category had a similar range of values (see Figure 1).

To determine if relationships between bird abundance and reproductive success were affected by choice of survey technique, I compared the ranks of plots based on bird abundance determined from point-count surveys to the ranks of plots based on bird abundance determined from spot-mapping. Only species with positive associations between bird abundance and number of nesting pairs were analyzed. Results were considered significant when $P<0.10$ for all statistical tests.

RESULTS

Bird Abundance and Number of Nesting Pairs

I located 58 nests in 1993 and 119 nests in 1994. The reliability of my findings depends on the assumption that I located nearly all nests of each species on each plot. I am confident that I met this assumption for American robins, pygmy nuthatches, solitary vireos, white-breasted nuthatches, and western bluebirds because observers were consistently able to locate nests of all individuals observed carrying nesting material or food. In contrast, I could not locate nests for all dark-eyed juncos observed performing nesting behaviors. Also, I often observed junco pairs and fledglings in areas where few or no nests were found. Therefore, I excluded juncos from my analyses.

Comparisons of ranks for bird abundance and number of nesting pairs (Table 1) yielded positive associations for solitary vireos ($r=0.457$, $P<0.05$), pygmy nuthatches (individuals $r=0.362$, $P<0.1$; and groups $r=0.621$, $P<0.01$), and western bluebirds ($r=0.374$, $P<0.1$). I found no association between bird abundance and number of nesting pairs for American robins ($r=0.287$, $P>0.1$) and white-breasted nuthatches ($r=0.340$, $P>0.1$).

Bird Abundance and Reproductive Success

Choice of survey technique did not significantly affect how plots were ranked based on bird abundance for solitary vireos ($P<0.05$), western bluebirds ($P<0.1$), and pygmy nuthatches ($P<0.05$). Therefore, results of comparisons between bird abundance and reproductive success would be similar whether abundance is estimated using spot-mapping or point-counts.

Relationships between bird abundance and reproductive success varied among the 3 species examined (Figure 1). Reproductive success was similar among abundance categories for solitary vireos ($P>0.1$); but varied among abundance categories for pygmy nuthatches ($P<0.05$) and western bluebirds ($P<0.05$).

DISCUSSION

Bird Abundance and Number of Nesting Pairs

Surveys based primarily on detection of songs may not reflect abundance of breeding individuals. Some surveys may be biased towards non-breeding individuals because unmated males may sing more vigorously than mated males (Von Haartman 1956, Baskett et al. 1978). Wilson and Bart (1985) found that song frequency in male house wrens (*Troglodytes aedon*) was lower in mated males from nest building through the fledgling period than in unmated males. For species in which non-breeding males are more easily detected than breeding males, measures of abundance alone would be inappropriate indices of habitat quality during the breeding season.

Ability to detect mated male birds depends largely on the behavior of individual species. In my study, mated males of species that showed positive associations between abundance and number of nesting pairs (i.e., solitary vireo, pygmy nuthatch, and western bluebird) were more vocal or visible than mated males of species that showed no association between abundance and number of nesting pairs (i.e., American robin and white-breasted nuthatch). Male solitary vireos continued to sing loudly while nest building and incubating. Pygmy nuthatches did not have a definite song, but their vocalizations around nest trees were loud and frequent. Male western bluebirds rarely sang during survey hours and had soft calls, but were highly visible due to their bright plumage and frequent movement at mid-canopy level. Male American robins and white-breasted nuthatches sang infrequently and were detected largely by low-volume calls. That I located 1 robin nest in a plot where no robins were detected during point-counts, is evidence that mated male robins were difficult to detect during point-counts.

If surveys are biased toward unmated males for American robins and white-breasted nuthatches, lack of association between bird abundance and number of nesting pairs for these species may indicate inconsistent ratios of breeding to non-breeding individuals among plots and years. O'Conner (1980) studied kestrels (*Falco tinnunculus*) in Britain and found that the proportion of non-breeders increased as the population increased. Non-breeding birds are more frequently associated with low quality habitats than are breeders (Atwood 1980, O'Conner 1981).

The reliability of bird abundance as an indicator of habitat quality for breeding birds may be associated with species characteristics. Van Horne (1983) predicted that species demonstrating social dominance interactions, high reproductive capacity, and generalist habits would be less likely to show positive association between abundance and habitat quality. All of the species I studied are territorial. The only clear generalist is the American robin. I ranked the 5 species in order of increasing reproductive capacity (western bluebird < solitary vireo < white-breasted nuthatch < pygmy nuthatch < American robin) measured by average clutch size and number of broods (Ehrlich 1988), to predict increasing probability that estimates of abundance will fail to reflect number of nesting pairs. These predictions match my results with the exception of pygmy nuthatches. Although pygmy nuthatches rank second to highest among the 5 species in reproductive capacity, the social interactions that would normally be expected to create a pool of dispersing subordinates instead result in the retention of subordinate individuals as helpers in a cooperative breeding system (Ehrlich 1988).

Bird Abundance and Reproductive Success

Relationships between bird abundance and reproductive success varied among the 3 species that showed positive associations between bird abundance and number of nesting pairs. One species, solitary vireo, showed constant reproductive success over all abundance categories. Similarly, Vickery et al. (1992a) reported no difference in reproductive success among areas with low, medium, and high density of territories of Vesper's sparrows.

Pygmy nuthatches showed increased reproductive success as abundance increased, but reproductive success of western bluebirds was lowest at medium abundance. Krebs(1971) found higher reproductive success at higher densities of great tits (*Parus major*). Vickery et al. (1992a) observed variation in reproductive success with territory densities for 2 species of grassland sparrows. Grasshopper sparrows (*Amodramus savannarum*) showed lowest reproductive success at low territory densities and highest success at medium territory densities. Reproductive success of Savannah sparrows (*Passerculus sandwichensis*) declined as territory density increased.

The variety of relationships between bird abundance and reproductive success among species might be explained by availability and quality of habitat patches within plots. Availability of habitat likely determines maximum occupancy for each species in each plot. Reproductive success would be expected to increase with increased quality of habitat patches. If quality of habitat patches is similar among plots but number of habitat patches varies, then a pattern similar to the one I observed for solitary vireos might occur -- uniform reproductive success with varying abundance. If quality as well as availability of habitat patches varies among plots, then a variety of other patterns could occur, including those I observed for pygmy nuthatches and western bluebirds -- high abundance of birds with high reproductive success and low to moderate abundance of birds with lower reproductive success (Figure 2).

Some information suggests that density-dependent factors may reduce reproductive success in high quality habitat. Vickery et al. (1992a) suggested that in some cases, birds may achieve similar reproductive success whether they breed in less densely occupied lower quality habitat or in preferred habitat where bird abundance is high. O'Conner (1981) found that great tits experience reduced clutch size and rearing success, as well as survival, under high population densities associated with preferred woodland habitats. Krebs (1971), however, found the opposite relationship for the great tit in similar habitats, indicating that the influences of density-dependent factors on reproductive success are inconsistent and not well understood.

Assessment of habitat quality for breeding birds may be further complicated by the scale of investigation (Wiens et al. 1987). Quality of habitat within study plots may vary at the level of territories. Vickery et al. (1992a) found clear differences in vegetative cover between high-success territories and low-success territories or unoccupied areas for 3 species of grassland sparrows. Habitat quality of study plots may also be affected by resources found in surrounding areas. Tobalske (1992) suggested that productivity of red-naped sapsuckers (*Sphyrapicus nuchalis*) in logged areas was dependent on use of resources from surrounding unlogged forest.

Management Implications

How well results from standard survey techniques indicated number of nesting pairs and reproductive success in this study appeared to be species specific. Other studies of relationships between bird abundance and reproductive success suggest that such relationships could be expected to vary under different circumstances for a single species. Thus, in a given time and place, abundance alone may be a reliable indicator of habitat quality for some species but not for others.

It would be useful for management purposes to predict whether bird abundance will reflect habitat quality for a given species. Singing behavior, social interactions, degree of specialization, and reproductive capacity of a species may provide some clues about the relationship between abundance and habitat quality, but should not be relied upon without further investigation.

The inability of bird abundance to reflect number of nesting pairs and reproductive success for some species may indicate complications of scale of habitat assessment (Wiens et al. 1987, Maurer 1986). Ideally, assessment of habitat quality for breeding birds should be conducted at several scales, from that of individual territory to landscape. Assessment of habitat quality at multiple levels, however, is more complicated, expensive, and time-consuming than more general assessments. Given the complexity and unpredictability of relationships between bird abundance and habitat quality, measures of reproductive success and potentially survival should be used in combination with measures of abundance to determine habitat quality for breeding birds, especially for species of management concern.

Table 1. Corresponding ranks of plots, based on number of nesting pairs (n) and bird abundance (a) in ponderosa pine forest of northern Arizona in 1993 and 1994. Ranks of plots area listed in order of increasing number of nesting pairs for each species. Abundance is based on all adults for American robin, western bluebirds, and white-breasted nuthatch; groups for pygmy nuthatch; and singing males for solitary vireo. Ranks in parenthesis represent the average rank of tied values in a given column. Total number of nests located in all plots is given for each species.

American Robin (12 nests)		Pygmy Nuthatch (75 nests)		Solitary Vireo (11 nests)		Western Bluebird (46 nests)		White-breasted Nuthatch (16 nests)	
n	a	n	a	n	a	n	a	n	a
(2.0)	(2.0)	1.0	(1.5)	(1.5)	(3.0)	1.0	(3.0)	(2.5)	2.0
(2.0)	(7.5)	2.0	(4.0)	(1.5)	(5.5)	2.0	(11.5)	(2.5)	(7.0)
(2.0)	(11.5)	(4.0)	(1.5)	(6.0)	(9.0)	(3.5)	(3.0)	(2.5)	(3.5)
(6.5)	(2.0)	(4.0)	(9.0)	(6.0)	(13.0)	(3.5)	(5.5)	(2.5)	(12.5)
(6.5)	(11.5)	(4.0)	(4.0)	(6.0)	(5.5)	(5.5)	(14.5)	(8.5)	1.0
(6.5)	(4.5)	(6.5)	(9.0)	(6.0)	(9.0)	(5.5)	(8.0)	(8.5)	5.0
(6.5)	(7.5)	(6.5)	(9.0)	(6.0)	(13.0)	7.0	(5.5)	(8.5)	15.0
(6.5)	(15.0)	8.0	(9.0)	(6.0)	(3.0)	(9.5)	1.0	(8.5)	(9.5)
(6.5)	(4.5)	9.0	(9.0)	(6.0)	1.0	(9.5)	(11.5)	(8.5)	(3.5)
(13.0)	(11.5)	(10.5)	(14.0)	(13.0)	(13.0)	(9.5)	(11.5)	(8.5)	(12.5)
(13.0)	(15.0)	(10.5)	(9.0)	(13.0)	(9.0)	(9.5)	(8.0)	(8.5)	(12.5)
(13.0)	(15.0)	(12.5)	(14.0)	(13.0)	15.0	(13.0)	(14.5)	(8.5)	(9.5)
(13.0)	(2.0)	(12.5)	(14.0)	(13.0)	16.0	(13.0)	(8.0)	(14.5)	(7.0)
(13.0)	(7.5)	(14.5)	(9.0)	(13.0)	(3.0)	(13.0)	(3.0)	(14.5)	(12.5)
(13.0)	(7.5)	(14.5)	16.0	(13.0)	(9.0)	(15.5)	(11.5)	(14.5)	16.0
(13.0)	(11.5)	16.0	(4.0)	(13.0)	(9.0)	(15.5)	16.0	(14.5)	(7.0)

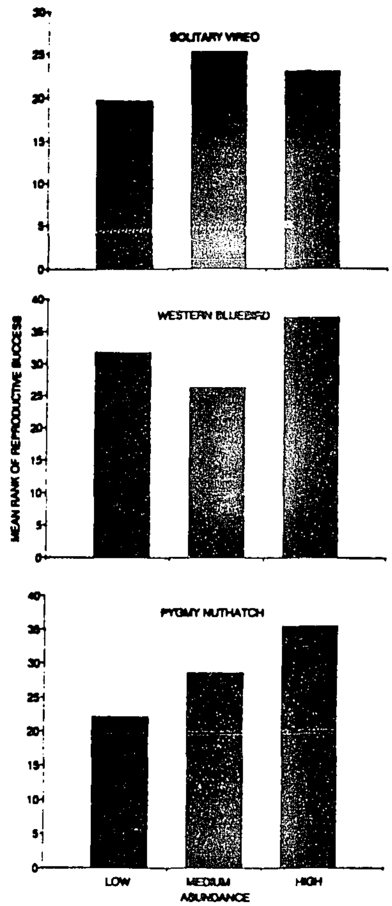

FIGURE 1. Mean rank of reproductive success among plots grouped into low, medium and high abundance of birds in ponderosa pine forest of northern Arizona in 1993 and 1994. Mean ranks were determined by ranking territories among all plots according to reproductive success for each species and averaging the ranks within a given abundance category. Abundance categories were derived from the number of territories identified by spot-mapping. Number of territories range from 1 - 2 for low, 3 - 5 for medium, and 6 - 7 for high abundance of solitary vireo; from 1 - 6 for low, 7 - 11 for medium, and 12 - 17 for high abundance of pygmy nuthatch; and from 1 - 3 for low, 4 - 6 for medium, and 7 - 9 for high abundance of western bluebird. Mean ranks were different among abundance categories for western bluebirds ($P<0.05$) and pygmy nuthatches ($P<0.05$), but not for solitary vireos ($P>.10$) (Kruskal-Wallis test).

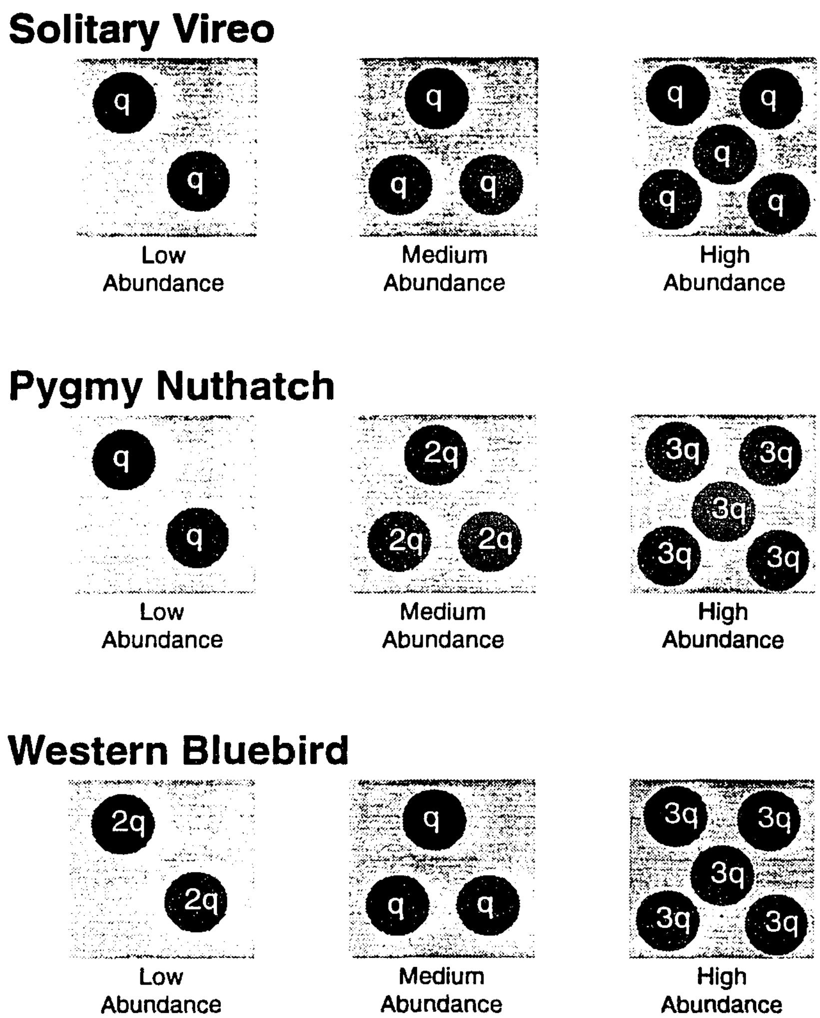

FIGURE 2. Schematic diagram of relationships between bird abundance, reproductive success, and habitat availability and quality. Each square represents a 16 ha plot. For each species, abundance would be expected to increase with the number of habitat patches (represented by the number of dark circles), while reproductive success would be determined by the quality of patches, (represented by the coefficient of 'q'). The above patterns may explain observations of equal reproductive success over varying abundance of solitary vireos; increased reproductive success with increased abundance of pygmy nuthatches; and lowest reproductive success at medium abundance and highest reproductive success at high abundance of western bluebirds.

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