

FIDELITY TO BREEDING TERRITORY IN A POPULATION OF RED-TAILED HAWKS

STEWART W. JANES

ABSTRACT.—Fidelity to breeding territories was examined on 33 Red-tailed Hawk (*Buteo jamaicensis*) territories in Oregon from 1973 to 1982 using the incidence of plumage dimorphism and mortality rates. Evidence suggested a high rate of return to previously occupied territories by females. The rate of change in the color morphs within territories among years was consistent with mortality rates alone. Alternative interpretations involving males' choice of mates with respect to female color and females' selection of habitat with respect to their color were explored. The first possibility, coupled with strong site fidelity by males could not be ruled out although it would require a high degree of color morph preference. No evidence for correlation between female territory selection and color was found.

Plumage dimorphism among males occurred too seldom to permit evaluation of breeding site fidelity among males at the population level. Several distinctively marked males were seen, however, to return to previously occupied territories.

Hawks are commonly assumed to breed repeatedly on the same territory (Newton 1979). Little evidence for such fidelity exists, however, beyond anecdotes involving a few distinctively marked or otherwise unique individuals. The few recent studies involving marked birds suggest varying degrees of fidelity to breeding territory among species and even sexes (see Newton 1979 for a review). Such behavior has been documented by marked birds in at least three *Buteo* species (*B. galapagoensis*, de Vries 1975; *B. platypterus*, Matray 1974; *B. regalis*, Schmutz and Schmutz 1981). Observations of distinctively marked individuals have disclosed territory fidelity among Red-tailed Hawks (*Buteo jamaicensis*; Fitch et al. 1946, Craighead and Craighead 1956). The data for these species do not indicate the degree to which territory fidelity occurs in populations because movements between territories are more likely to pass undetected. I report here on breeding territory fidelity in a population of Red-tailed Hawks, identified with the use of plumage dimorphism.

STUDY AREA AND POPULATION

Thirty-three territories were monitored by me and from one to six assistants between 1973 and 1982 on a 137-km² study area in southeastern Wasco County, Oregon. The native vegetation is characteristic of the Columbia Basin Province (Franklin and Dyrness 1973) and forms a mosaic of habitats dominated by bunchgrass (*Agropyron spicatum* and *Festuca idahoensis*) or sagebrush (*Artemisia tridentata*). Dryland wheat farming and grazing, however, have altered much of the native vege-

tation. In many areas introduced annual grasses (*Bromus tectorum* and *Elymus caput-medusa*) and certain shrubs (*Chrysothamnus nauseosus*, *C. vicidiflorus*, and *Gutierrezia sarothrae*) are locally dominant.

The Red-tailed Hawks in this study area were dimorphic, 18% (64/358) of the bird-years being represented by dark-phase individuals. One bird residing on a territory during a breeding season represents one "bird-year." Dark-phase birds were mostly dark below with little or no contrast between the breast and the abdominal band; from beneath, the dark wing-lining contrasted sharply with the much paler remiges. Light-phase birds were predominantly white or cream-colored beneath, including the wing-lining and remiges, with a contrasting abdominal band of varying extent. Although light- and dark-phase birds varied considerably, I was able to classify all but one individual into one category or the other. The exceptional bird was an erythristic female, present for three breeding seasons, whom I classified as dark-phase.

METHODS

Territorial boundaries were relatively stable from year to year (Janes 1984). Thus the coloration of the occupants of a given territory could be recorded yearly. I ascertained the sexes of the hawks either by the birds' position during copulations or by a combination of characters including relative size (female generally larger), incubation duties (female does more; Janes, unpubl. data), nest attentiveness after hatching (female greater; Stinson 1980), response to congeneric territorial intruders (male initiates more encounters; Janes, unpubl. data),

TABLE 1. Observed and expected color-phase sequences of female Red-tailed Hawks within territories in Oregon among years (1973–1982). Expected values assume complete territory fidelity and are based upon an annual mortality rate of 0.206 (Henny and Wight 1972) and a 0.260 observed incidence of dark-phase females.

Color phase		Number observed	Prob. of survival		Prob. of replacement	Freq. expected	Number expected
Initial	Subsequent						
Light	Light	98	.794	+	.152	= .946	100.3
Light	Dark	8	0	+	.054	= .054	5.7
Dark	Dark	28	.794	+	.054	= .848	26.3
Dark	Light	3	0	+	.152	= .152	4.7
Total		137					137.0

$\chi^2 = 1.71, df = 3$
 $P > 0.05$

and response to humans near the nest (female more aggressive; Fitch et al. 1946). I include only those results where the determination of sex was reasonably certain.

Presence of a male or a female of the same color morph on a territory in succeeding years allowed two possible explanations: either it was the same individual or it was replaced by another individual of the same color morph, in turn either through mortality or movement to another area by the original bird. When an individual of one color morph was succeeded by an individual of a different color morph, I assumed replacement. Using the annual adult mortality rate for Red-tailed Hawks north of 42°N (0.206; Henny and Wight 1972) and the frequency of light- and dark-phase birds in the population, I calculated the probabilities of changes in coloration of territorial residents assuming no movement between territories. A rate of change, in the color morph of individuals occupying territories, that was greater than predicted was taken as evidence for such movement, which I evaluated by a chi-square goodness-of-fit test.

The use of the mortality rate presented by Henny and Wight (1972) assumes equal mortality rates between sexes. However, Reynolds (1972) suggested that adult accipiters may experience sexually differing mortality rates. This would not be surprising considering their high degree of sexual differences in ecology and morphology. Evidence for differential mortality rates is weak, however, particularly in *Buteo* (Snyder and Wiley 1976), possibly indicating that differences, if any, are relatively small. Red-tailed Hawks are much less sexually dimorphic than accipiters (Snyder and Wiley 1976), and I have assumed equal mortality rates between sexes.

RESULTS AND DISCUSSION

The observed rates of change in the color morphs of Red-tailed Hawks were consistent with the expected results based solely upon the

mortality rate (Henny and Wight 1972) (Table 1). Thus, I found no evidence to suggest that female Red-tailed Hawks moved among territories between years. Because the actual mortality rate for adults in this population is unknown, I tested the robustness of the above results by varying the mortality rate. This result was unaffected by a potential error in the estimated mortality rate of ± 0.050 ($\chi^2 = 1.88$ and 3.43, $P > 0.05$).

I could not assess the rate of movement of males among territories because dark-phase males were few, with only 3.6% male-years involving such individuals. I could sometimes recognize individual males by distinctive plumage; these birds returned to the same territory in each case ($n = 18$, 1 each for 3, 4, and 5 years and 3 for 2 years).

The assignment of individuals to a particular sex was not without potential error. As a check, I performed a second test in which I treated pairs as a unit consisting of the various color-phase combinations. The results were again consistent with mortality rate alone (Table 2), giving no indication of movement between territories. The results were also unaffected by a potential error in the estimate of annual adult mortality rate of ± 0.050 ($\chi^2 = 3.82$ and 1.95, $P > 0.05$).

The analyses assumed not only equal mortality rates between sexes, but also that matings were random with respect to color morph. Random mating with respect to color morph has been found among Ferruginous Hawks (*Buteo regalis*; Schmutz and Schmutz 1981), but Dunkle (1977) encountered assortative mating among Swainson's Hawks (*B. swainsoni*). Since both members of a pair of Red-tailed Hawks are unlikely to die during the same year ($P = 0.042$), we can assume that a given individual typically takes more than one mate during its lifetime. Preference by males for a mate of a particular color morph would tend to mask interterritorial movements by females, potentially producing artificially high

TABLE 2. Observed and expected color-phase sequences in Red-tailed Hawk pairs within territories in Oregon among years (1973–1982). Expected values assume complete territory fidelity and are based upon an annual mortality rate of 0.206 and an incidence of dark-phase birds of 0.179.

Initial pairing	Subsequent pairing			Total	Subsequent pairings involving	
	D × D ^a	D × L	L × L		Change	No change
Observed						
Dark × light	1	34	3	38	4	34
Light × light	0	8	96	104	8	96
Total				142		
Expected						
Dark × light	1.1	30.6	6.2	37.9	7.3	30.6
Light × light	0.1	7.3	96.4	103.8	7.4	96.4
Total				141.7		
					$\chi^2 = 1.92, df = 3$	$P > 0.05$

^a D = dark-phase, L = light-phase.

estimates of female territory fidelity. The low incidence of plumage dimorphism in males in my study area allowed little choice by females. If females are not faithful to territories but males do choose mates with respect to color, the results become an estimate of male fidelity to territories. However, the degree of mate preference by color becomes important. "Mistakes" in the choice of mates or the lack of mate preference by males with respect to color would produce more changes in the color morphs of females on territories than expected by chance alone. Male choice of mates would have to be expressed at least 88% of the time to obtain a chi-square value suggesting a lack of interterritorial movements. Although this interpretation cannot be ruled out, it requires relatively stringent conditions. I find it more parsimonious to interpret my results in terms of female fidelity to territory.

Another possible interpretation involves habitat selection by females based on their color. Non-random replacement of birds with respect to color could lead to biased estimates of territory fidelity. Preston (1980) found that Red-tailed Hawks of different color morphs selected different foraging sites. If female color is correlated with habitat, more territories would be expected to be inhabited by females of a single color morph than would be expected by chance. I assessed this by using the incidence of plumage dimorphism and the mortality rate, and found no evidence for habitat selection with respect to color (Table 3). While my results suggest a high rate of fidelity to territories by female Red-tailed Hawks, they do not preclude interterritorial movements. If such movements do exist, they are at too low a rate to be detectable by the tests I employed.

The apparent high degree of territory fidelity among female Red-tailed Hawks is somewhat

surprising. Territory quality (measured in terms of long-term fledging rates) varied widely in my population (Janes 1984). Thus interterritorial movements by birds attempting to gain better territories might have been anticipated. Work with the Eurasian Sparrowhawk (*Accipiter nisus*; Newton and Marquiss 1976) revealed varying degrees of territory fidelity. Females who occupied high-quality territories (measured in terms of the occupancy rate and the previous year's reproductive success) remained there more than those inhabiting poorer territories. Cavé (1968) reported similar results with Eurasian Kestrels (*Falco tinnunculus*), although fidelity varied annually

TABLE 3. Test for non-random choice of territories by female Red-tailed Hawks with respect to their color morph in Oregon (1973–1982). The lack of significant difference between the observed and expected values suggests that territory choice was random with respect to color.

Number of females on a territory (n)	Expected no. of territories with n females ^a	Probability of both dark- and light-phase females ^b	Expected no. of territories with both color phases	Observed no. of territories with both color phases
1	12.5	×	.000	= 0
2	10.7	×	.385	= 4.1
3	6.5	×	.577	= 3.8
4	2.4	×	.696	= 1.7
5	0.7	×	.777	= 0.5
6	0.1	×	.835	= 0.1
Total	32.9			10.2 11
			$\chi^2 = 0.08$	$df = 1$ $P > 0.05$

^a Figures were derived from the number of years of observation for respective territories and the equation, $P(k) = \binom{r}{k} P^k (1-P)^{r-k}$, where $P(k)$ is the probability of k deaths in $r + 1$ years of observation, and P is the mortality rate. The number of females that have inhabited a territory is $k + 1$.

^b The probability of observing females of both color phases on a territory is $1 - (j^n + (1-j)^n)$ where j is the frequency of dark-phase females in the population and n is the number of females having inhabited a territory.

in relation to densities of common voles (*Microtus arvalis*). These findings suggest that the probability of gaining a good territory initially may be low. Even relatively poor territory, however, presents an opportunity for reproduction and is therefore of considerable value. Furthermore, these observations suggest that the risk of losing a territory while attempting to secure a better one may be relatively high.

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Biology Department, University of California, Los Angeles, California 90024. Received 3 February 1983. Final acceptance 8 September 1983.