Sex-biased Dispersal of Young Western Screech-owls (*Otus kennicottii*) in Southwestern Idaho

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Abstract.—We examined dispersal distance of young Western Screech-owls (*Otus kennicottii*) from nest sites to overwintering sites in relation to two hypotheses for sex-biased dispersal. Overall, young Screech-owls (N = 31) dispersed an average of 10.6 ± 1.8 km to overwintering sites, and females (14.7 ± 2.5 km; N = 13) dispersed farther than males (5.1 ± 2.3 km; N = 15). This result is not consistent with the behavioral dominance hypothesis, which predicts that individuals of the more dominant sex class (apparently females in Western Screech-owls) should be more philopatric. The mating system hypothesis, which predicts that the sex that establishes the territory should disperse shorter distances, remains tenable as an explanation for female-biased dispersal in Western Screech-owls.

Among the curious features of avian dispersal is that it is often gender biased; that is, females usually disperse more frequently or farther than males (Gauthreaux 1978, Greenwood 1980). The causes of differential dispersal are not well understood (Pusey 1987), but hypotheses that attempt to explain this pattern are common (Johnson and Gaines 1990). Two such hypotheses are (1) the behavioral dominance hypothesis (Gauthreaux 1978), which predicts that individuals of the dominant sex class force subordinates to disperse farther, and (2) the mating system hypothesis (Greenwood 1980), which argues that selection has favored philopatry among individuals of the sex that defends resources (e.g., territories) and that inbreeding avoidance causes greater dispersal of the sex being attracted. For most species of birds the two hypotheses make identical predictions. Because males typically defend territories, and males are generally dominant to females, both hypotheses predict female-biased dispersal in these species. However, the two hypotheses can be distinguished by examining a species in which males establish and defend territories but in which typical dominance patterns are reversed, so that females dominate males. In this case, the hypotheses make contrasting predictions, and the relative importance of dominance patterns and mating systems in leading to sex-biased dispersal patterns can be assessed.

The Western Screech-owl (*Otus kennicottii*) is one species of bird that appears to fit these criteria. Males select and defend territories, but pat-terns of size dimorphism are reversed from the typical pattern in passerines, for example, so that female Screech-owls are larger than males (Dimorphism Index = 2.3; Johnsgard 1988). Size is often an important predictor of domin-ance status in raptors that display reversed sexual dimorphism, including owls (Boxall 1979, Evans 1980, Keith 1964, Mueller 1986). Moreover, in an earlier study we found that the most dominant Western Screech-owl nestlings tended to be larger than their subordinate siblings, and females tended to weigh more than males (Ellsworth and Belthoff, in prep.). Thus, it is probably safe to assume that the large size of female Western Screech-owls confers upon them a competitive advantage over smaller males. Under this scenario, the behavioral dominance hypothesis predicts that females will outcompete subordinate males for available resources and effectively force males to disperse farther from the natal area. Domin-ant females also may aggressively chase less dominant males from the natal area. Either way, this contrasts with the mating system hypothesis which predicts that male Western Screech-owls, which establish and defend territories, should be more philopatric than females.

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In this study, we examined the dispersal behavior of young Western Screech-owls in relation to the behavioral dominance and mating system hypotheses. The distance of dispersal was measured from the natal area to the apparent overwintering site acquired by the dispersing young; thus, dispersal distances reported here do not represent natal dispersal distances (i.e., distance from natal to first breeding site). However, these initial movements are important in the lives of young Western Screech-owls because they represent a significant component of the dispersal process, and settlement opportunities likely decline later in the year when suitable habitats become saturated with dispersers. Furthermore, the initial stage of dispersal may be representative of final dispersal because at least some juveniles breed in the same areas in which they settled to overwinter (see Belthoff and Ritchison 1989), and adults breed in the same area in which they winter, (i.e., they are territorial residents throughout the entire year).

METHODS

Study Area

The study area included a 53 km stretch of the Snake River in Elmore and Owyhee Counties in southwestern Idaho, which included part of the Snake River Birds of Prey National Conservation Area and encompassed C.J. Strike Reservoir and portions of the Bruneau River. Here, the Snake River has carved a canyon of up to 125 m high. Above the canyon on the Snake River Plain, vegetation is characteristic of a shrub-steppe desert, and trees are largely absent. Below the canyon rim the river meanders beneath vertical volcanic cliffs and through wide terraces of the old river bed and ancient lakes. Native cottonwoods (*Populus balsamifera*), willows (*Salix* spp.), and introduced Russian olives (*Eleaegnus angustifolia*), black locusts (*Robinia pseudoacacia*), and boxelders (*Acer negundo*) grow along the Snake and Bruneau rivers in seeps and tributaries, and near farms. In these riparian habitats and woodlots, Western Screech-owls nest in natural cavities or in wooden nest boxes erected by the Bureau of Land Management.

Transmitter Application and Monitoring

Approximately 1 week prior to fledging, Western Screech-owl nestlings were fitted with radio-transmitters (Model SOPB 2190; Wildlife Materials, Carbondale, IL) and provided with a uniquely numbered aluminum leg band. At this time, we also collected blood from young with microhematicrit tubes following venipuncture of the alar vein with a microlancet, and stored the blood at -20°C until gender analyses were performed. Gender of young owls was subsequently determined by a commercial laboratory (Zoogen, Inc., Davis, CA) using DNA isolated from these blood samples.

We captured and affixed radio-transmitters to all juvenile Western Screech-owls (N = 48) in 15 families, with the exception of two juveniles that fledged before we could attach transmitters (one from Delta and one from Harris). The mean date that young left the nest box was 18 May (N = 50), ranging from 8 May to 4 June. Following fledging we located the diurnal roost sites of all radio-tagged young until they dispersed. Eight young died on the natal area before dispersing. Seven others disappeared early in the post-fledging period weeks before they should have dispersed and were assumed to be dead. Thus, we were able to monitor 35 young from fledging until dispersal. The number of days these young spent on the natal area ranged from 41-97 days (mean = 60.0 ± 2.36 [SE]), while the average dispersal date was 16 July (range: 25 June - 25 August).

To locate dispersing young, we conducted airplane searches within and outside of the boundaries of the study area. After each flight, we searched several times on the ground for juveniles located from the air. In 1994 and 1995, the initial searches were conducted on 12 July and 26 July, respectively. Subsequent aerial searches (29 August and 21 October 1994, and 13 September 1995) were conducted to locate later dispersers and track juveniles as they settled into overwintering sites. Young were relocated from the ground periodically throughout the fall until mid-November, and the last place (within an approximately 100 m radius) that young were located was considered to be their dispersal site. We considered young to be settled if they occupied a single site for at least 3 consecutive weeks, or if they changed sites early in the dispersal period but were located again in late autumn at a time when most other young had apparently settled.

Statistical Analyses

Using analyses of variance (ANOVA), we examined the effect of sex on dispersal distance of

young by comparing the distance that males and females traveled from their natal area to apparent overwintering sites. Because young within a brood may not disperse independently of one another, we performed an additional analysis while blocking by brood. This analysis included only young from mixed-sex broods and for young which were located on dispersal areas (N = 6 broods).

RESULTS

We located 31 of 35 (88.6 percent) young that survived the postfledging period after they dispersed. Twenty-eight young were considered to be settled in a dispersal area because they occupied a particular site for a minimum of 3 weeks (N = 25), or were found late in the autumn at a time in which other young were apparently settled (N = 3). Considering all individuals, the average dispersal distance was 10.6 ± 1.8 (SE) km (range: 0.7-36.1; N = 31; table 1) from the nest site to the last place young were located 4-12 weeks after disper-sal. All analyses based on these data indicate that females dispersed farther than males. For example, among settled young (N = 28), females (14.7 ± 2.5 km; N = 13) were located farther from the nest than males (5.1 ± 2.3 km; N = 15; fig. 1), and the difference between the sexes was significant ($F_{1,26}$ = 7.95, p = 0.009). When only juveniles from mixed-sex broods (N = 19 owls from six broods) were considered (i.e., so that blocking by family could be accomplished to remove inter-family differences from the analysis), the average dispersal distance in females (16.4 ± 3.0, N = 10) also was greater than for males (6.0 ± 3.1, N = 9), although the difference was significant at a slightly higher alpha value ($F_{1,12}$ = 4.28, p = 0.06) than when all juveniles were considered. Finally, three young were located only once from an airplane by their transmitter signal, so their over-wintering sites were not confirmed. Nonetheless, even among these "unknown" birds, females (N = 2) were farther from their natal areas the only time they were located (27.6 and 18.8 km) than was the single male (14.7 km; table 1), which is consistent with the results from young that were known or presumed to have settled and the conclusion that females of this species disperse farther than males.

DISCUSSION

Our results suggest that young female Western Screech-owls dispersed farther than males,

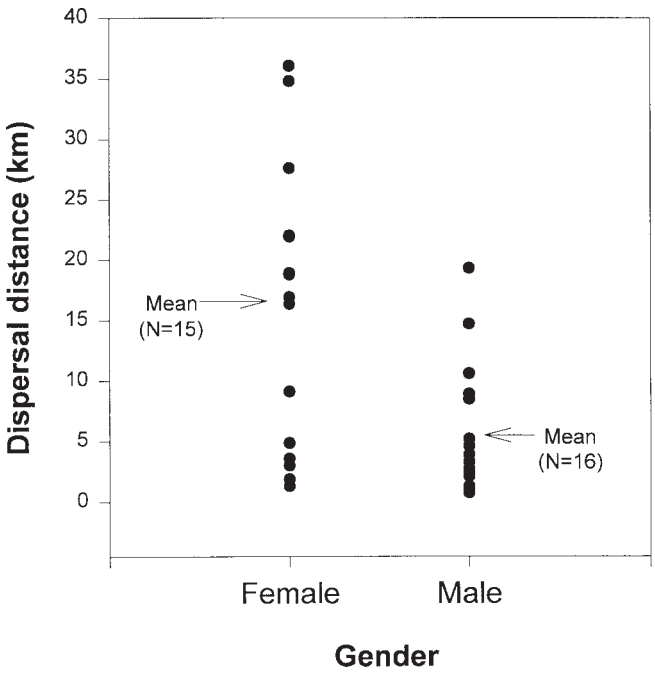

Figure 1.—*Dispersal distances from the natal area to apparent overwintering sites of female (N = 15) and male (N = 16) Western Screech-owls in southwestern Idaho in 1994 and 1995.*

which is consistent with the general pattern of female-biased dispersal in birds (Greenwood and Harvey 1982). It is important to note that the dispersal distances reported here for young Western Screech-owls (with one exception) are based on distances between natal and over-wintering sites rather than between natal and first breeding sites. We were unable to locate the first breeding sites for most owls in the study because the radio-transmitters could not be designed to function long enough. Nonetheless, the information we obtained is valuable because it suggests that differences in distances moved by young males and females during the dispersal process may be established long before the breeding season arrives.

If our assumption concerning patterns of dominance between sex classes in Western Screech-owls is correct, and because females dispersed farther than males, the behavioral dominance hypothesis does not appear to explain the patterns of sex-biased dispersal among Western Screech-owls in our study. Instead, the results are more consistent with the mating system hypothesis which predicts that males are more philopatric than females in

Table 1.—*Dispersal distances from the natal area to apparent overwintering sites of young Western Screech-owls (N=31) in southwestern Idaho in 1994 and 1995. A settled fate indicates that young were apparently settled in one area, as they were either located more than once or were located late in the autumn at a time when most other young were settled. An unknown fate indicates that young were only located once in a dispersal area.*

Family	Bird	Sex	Distance	Fate
	Number		*km*	
1994				
Cabin	103	male	4.6	Settled
	104	female	36.1	Settled
	105	female	18.8	Unknown
	106	female	4.9	Settled
	107	female	16.9	Settled
Bruneau Marsh	108	male	0.7	Settled
	109	female	3.0	Settled
	110	male	2.7	Settled[a]
	111	male	8.5	Settled
Rabbit Springs	112	female	16.4	Settled
	113	female	1.3	Nesting[b]
Trueblood	128	male	3.3	Settled
	130	male	3.9	Settled
	131	male	2.7	Settled
Boat Launch	100	male	0.9	Settled
	120	male	10.6	Settled
Treeline	136	female	27.6	Unknown
1995				
Cellar Hole	154	female	21.9	Settled
	156	female	18.9	Settled
	157	male	19.3	Settled
Upper Cabin	167	male	2.1	Settled
	170	male	14.7	Unknown
Cabin	172	female	22.0	Settled
	173	male	1.3	Settled
	174	male	5.2	Settled
Trueblood	159	male	2.5	Settled
	160	female	1.9	Settled
	171	female	3.6	Settled
CJ Strike	164	female	34.8	Settled[a]
	165	male	8.9	Settled[c]
Harris	498	female	9.1	Settled

[a] Considered to be settled because young were located in late fall at a time in which other young were settled
[b] Bred as 1-year-old.
[c] Apparently killed by a car in mid-October.

monogamous species and in which males defend territories (Greenwood 1980), like Western Screech-owls. Greenwood (1980) suggests that in these species males establish territories before females begin selecting a mate. Consequently, males settle closer to home in familiar habitat, while females do not have the costly constraint of establishing a territory. Instead, they have the capacity to choose among the available males and their territories, and females may settle farther away to avoid inbreeding (Greenwood 1980).

Although our results are more consistent with the mating system hypothesis than with the behavioral dominance hypothesis, female-biased dispersal in Western Screech-owls could be explained by factors we did not consider.

For example, sex-biased dispersal patterns may result from differential territory turnover for males and females (Waser 1985, Plissner and Gowaty 1996). That is, if one sex class vacates, through mortality or other factors, territories more frequently than the other, settlement opportunities would differ for dispersing males and females, and sex-biased dispersal patterns could result regardless of the particular mating system (Tonkyn and Plissner 1991). Unfortunately, we do not have sufficient demographic data from Western Screech-owls in our study area to evaluate this alternative hypothesis at this time.

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LITERATURE CITED

Belthoff, J.R.; Ritchison, G. 1989. Natal dispersal of Eastern Screech-owls. Condor. 91: 254-265.

Boxall, P.C. 1979. Aspects of the behavioral ecology of wintering Snowy Owls (*Nyctea scandiaca*). Calgary, Canada: University of Calgary. M.S. thesis.

Evans, D.L. 1980. Vocalizations and territorial behavior of wintering Snowy Owls. American Birds. 34: 748-749.

Gauthreaux, S.A., Jr. 1978. The ecological significance of behavioral dominance. In: Bateson, P.P.G.; Klopfer, P.H., eds. Perspectives in ethology. vol 3. New York: Plenum Press. 177-254 p.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour. 28: 1140-1162.

Greenwood, P.J.; Harvey, P.H. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics. 13: 1-21.

Johnsgard, P.A. 1988. North American owls, biology and natural history. Washington DC: Smithsonian Institute Press. 295 p.

Johnson, M.L.; Gaines, M.S. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annual Review of Ecology and Systematics. 21: 449-480.

Keith, L.B. 1964. Territoriality among wintering Snowy Owls. Canadian Field-Naturalist. 78: 17-24.

Mueller, H.C. 1986. The evolution of reversed sexual dimorphism in owls: an empirical analysis of possible selective factors. Wilson Bulletin. 98: 387-406.

Plissner, J.H.; Gowaty, P.A. 1996. Patterns of natal dispersal, turnover and dispersal costs in Eastern Bluebirds. Animal Behaviour. 51: 1307-1322.

Pusey, A.E. 1987. Sex-biased dispersal and inbreeding avoidance of birds and mammals. Trends in Ecology and Evolution. 2: 295-299.

Tonkyn, D.W.; Plissner, J.H. 1991. Models of multiple dispersers from the nest: predictions and inference. Ecology. 72: 1721-1730.

Waser, P.M. 1985. Does competition drive dispersal? Ecology. 66: 1171-1175.