

- Journal of Comparative Physiology A 172:295–301.
- MARHOLD, S., W. WILTSCHKO, AND H. BURDA. 1997. A magnetic polarity compass for direction finding in a subterranean mammal. *Naturwissenschaften* 84:421–423.
- MERKEL, F. W., AND W. WILTSCHKO. 1965. Magnetismus und Richtungsfinden zugunruhiger Rotkehlchen (*Erithacus rubecula*). *Vogelwarte* 23:71–77.
- MUNRO, U., J. A. MUNRO, J. B. PHILLIPS, AND W. WILTSCHKO. 1997. Effect of wavelength of light and pulse magnetisation on different magneto-reception systems in a migratory bird. *Australian Journal of Zoology* 45:189–198.
- PHILLIPS, J. B., AND S. C. BORLAND. 1992. Behavioral evidence for use of a light-dependent magneto-reception mechanism by a vertebrate. *Nature* 359:142–144.
- PHILLIPS, J. B., AND S. C. BORLAND. 1994. Use of a specialized magnetoreception system for homing by the eastern red-spotted newt, *Notophthalmus viridescens*. *Journal of Experimental Biology* 188: 275–291.
- QUINN, T. P. 1980. Evidence for celestial and magnetic compass orientation in lake-migrating sockeye salmon fry. *Journal of Comparative Physiology* 137:243–248.
- SCHULTEN, K., AND A. WINDEMUTH. 1986. Model for a physiological magnetic compass. Pages 99–106 in *Biophysical effects of steady magnetic fields* (G. Maret, N. Boccara, and J. Kiepenheuer, Eds.). Springer-Verlag, Heidelberg, Germany.
- WILTSCHKO, R., AND W. WILTSCHKO. 1978. Evidence for the use of magnetic outward journey information in homing pigeons. *Naturwissenschaften* 65:112.
- WILTSCHKO, R., AND W. WILTSCHKO. 1995. Magnetic orientation in animals. Springer-Verlag, Heidelberg, Germany.
- WILTSCHKO, R., AND W. WILTSCHKO. 1998. Pigeon homing: Effect of various wavelengths of light during displacement. *Naturwissenschaften* 85: 164–167.
- WILTSCHKO, W. 1968. Über den Einfluß statischer Magnetfelder auf die Zugorientierung der Rotkehlchen (*Erithacus rubecula*). *Zeitschrift für Tierpsychologie* 25:537–558.
- WILTSCHKO, W., U. MUNRO, H. FORD, AND R. WILTSCHKO. 1993. Red light disrupts magnetic orientation of migratory birds. *Nature* 364:525–527.
- WILTSCHKO, W., AND R. WILTSCHKO. 1981. Disorientation of inexperienced homing pigeons after transportation in total darkness. *Nature* 291: 433–434.
- WILTSCHKO, W., AND R. WILTSCHKO. 1995. Migratory orientation of European Robins is affected by the wavelength of light as well as by a magnetic pulse. *Journal of Comparative Physiology A* 177: 363–369.
- WILTSCHKO, W., AND R. WILTSCHKO. 1999. The effect of yellow and blue light on magnetic compass orientation in European Robins, *Erithacus rubecula*. *Journal of Comparative Physiology A* 184: 295–299.

Received 28 August 1998, accepted 25 June 1999.
Associate Editor: F. R. Moore

The Auk 117(1):260–264, 2000

Facultative Nest Switching by Juvenile Ospreys

LAUREN N. GILSON^{1,3} AND JOHN M. MARZLUFF^{2,4}

¹Raptor Research Center, Department of Biology, Boise State University, Boise, Idaho 83725, USA; and

²College of Forest Resources, University of Washington, Seattle, Washington 98195, USA

When fledglings forego parental protection and provisioning to explore nests other than their own, they take a behavioral risk. In species whose young

generally cannot leave the nest prior to developing flight, such movements among nests are unlikely to occur. Yet, this facultative behavior, which we refer to as “nest switching,” has been noted in a variety of semialtricial species (e.g. Poole 1982, González et al. 1986, Newton 1986, Bustamante and Hiraldo 1989, Donazar and Ceballos 1989, Kenward et al. 1993).

Two models may explain facultative nest switching in semialtricial species: (1) switching may arise

³ Present address: Department of Birds, Transvaal Museum, P.O. Box 413, Pretoria, South Africa. E-mail: gilson@tm.up.ac.za

⁴ Address correspondence to this author. E-mail: corvid@u.washington.edu

purely from random predispersal movements of fledglings; or (2) switching may be a nonrandom, deterministic behavior that is influenced by conditions that fledglings encounter in their natal nest. The deterministic model predicts that some fledglings are more likely to switch than others, based on parental provisioning and individual food intake prior to fledging, both of which may be affected by brood size. The random-movements model predicts no association between brood size or conditions within a nest and frequency of nest switching; rather, nest switching is influenced by opportunities available to a potential switcher (e.g. proximity and occupancy of nearby nests). The two models are not mutually exclusive, because spatial factors may influence the outcome of a behaviorally motivated switching attempt. However, the suite of predictions for each model should indicate whether the operant mechanism underlying nest switching is random or deterministic.

Facultative nest switching has been documented in several populations of Ospreys (*Pandion haliaetus*; Fernandez and Fernandez 1977, Judge 1981, Poole 1982). Through natural experiments and manipulations of Osprey broods in the field, we examined (1) the frequency of nest switching; (2) the effects of brood size on parental provisioning, nestling food intake, and nest switching; and (3) the influence of population density and dispersion on frequency of nest switching. Our objectives were to determine which fledglings switch nests and to assess factors that may explain why some fledglings switch while others do not.

Study area and methods.—We observed 20 pairs of Ospreys that nested on artificial platforms in three areas of Cascade Reservoir, west-central Idaho, during 1993 and 1994. To monitor food intake and individual behavior, we dyed the head feathers (random assignment of colors within broods) of 32 nestlings as soon as the nestlings were visible above the nest rim (10 days or older) and banded all young at 23 to 35 days of age using standard USGS bands and anodized numerical bands. We equipped 28 of 30 fledglings (two nestlings died) with necklace-mounted radio transmitters and fitted all fledglings in 1994 with both a transmitter and a color-coded patagial marker of rip-stop nylon (Gilson 1996).

To test the effects of brood size on food intake, parental provisioning, and ultimately on switching behavior, we augmented the number of three-young (3Y) broods in our sample by translocating nestlings among similarly aged broods (see Spitzer 1984). We observed three 3Y broods and seven one-young (1Y) broods in each year of study. We created two of the 3Y broods through translocation in 1993 and one in 1994. Translocated nestlings were chosen at random from a donor 2Y brood and placed into the nearest recipient 2Y brood ($\bar{x} = 1.07 \pm \text{SE of } 0.41 \text{ km}$ between nests) of similar age. We fostered young into recipi-

ent broods at 10 to 21 days of age to allow for a natural age/size range among new brood mates (Forbes 1991). Details of observations and measurements are provided in Gilson (1996).

To determine whether switching was a random movement, we used analysis of variance (ANOVA) to compare internest distances, nearest-neighbor distances, and number of occupied nests and vacant platform nests within a 2-km radius of nests that produced switchers with those of nests that did not produce switchers. We analyzed the use of perches by fledglings from 1Y versus 3Y broods using multivariate analysis of variance (MANOVA).

To assess whether switching behavior was determined by conditions at the nest prior to fledging (i.e. leaving the nest), we recorded parental provisioning rates and individual food intake (defined as bites per observation) of all juveniles in their nests. We assessed differences on two levels: 1Y versus 3Y broods, and among siblings (brood mates where manipulated) within 3Y broods. We assessed how brood size affected parental provisioning using a one-tailed ANOVA, with the expectation that nestlings in larger broods receive lower per capita provisioning than those in single-chick broods. To describe how individual food intake varied among the two experimental brood sizes, we compared mean food intake, variance in intake, and average minimum daily intake during the two weeks prior to fledging using MANOVA and assessed statistical significance of the MANOVA results with a Bonferroni-adjusted α based on the number of dependent variables. We used a Wilcoxon matched-pairs signed-rank test to assess whether the food intake of switchers differed from that of nonswitchers within 3Y broods; all food-intake measures were \log_{10} transformed.

To assess the effect of brood-size manipulation on relocation of individual nestlings, we compared switching frequencies of unmanipulated to manipulated broods and of resident to translocated nestlings using contingency analyses with Yates' correction for continuity. All analyses used data from both years to compare 1Y and 3Y broods. We used Mann-Whitney tests to assess factors at nests that affected the occurrence of switching. All tests were performed with SAS (1989) and are two-tailed unless stated otherwise; all means are reported $\pm \text{SE}$.

Results.—Nest switching was observed nine times among marked broods (Table 1) and four times involving unmarked individuals that joined marked broods. Switches occurred 0 to 23 days postfledging when juveniles were 54 to 72 days old ($\bar{x} = 66 \pm 4.1$ days). Switchers moved an average of 1.82 km overall ($\bar{x} = 0.92 \pm 0.2 \text{ km}$ between platform nests in local breeding areas, $n = 7$; $\bar{x} = 4.9 \pm 1.7 \text{ km}$ between platforms and remote nests, $n = 2$) and remained at recipient nests from 10 min to 21 days. Of the seven switches within local nesting areas, three resulted in stays of more than 24 h ($\bar{x} = 8.32 \pm 6.4$ days, $n = 3$),

TABLE 1. Summary of nest-switching events by Ospreys in west-central Idaho, 1993–1994.

Nest switcher	Natal brood size	Recipient brood size	Days postfledging	Distance moved (km)	Duration of stay	Stay over night ^a	Alloparental care ^a
PBP	3	1	0	1.49	25 min	N	N
GBG	3	1	1	0.53	<24 h	Y	Y
PGY	1	1	3	1.37	90 min	N	N
WC3Y	3	3	4	1.51	21 days	Y	Y
YGY	3	0	6	0.26	3 days	Y	Y
SL1P	3	2	≥14	0.96	10 min	N	N
SL1Y	3	2	15	6.70	≤6 days	U	U
WC3P	3	0	23	0.35	2 min	N	N
SE6	1	U	33	3.25	≥3 days	U	U

^a Y = yes, N = no, U = unknown.

and four resulted in toleration at the nest for less than 24 h ($\bar{x} = 5.04 \pm h$, $n = 4$).

Five fledglings switched nests within one week after fledging (early season, $\bar{x} = 2.2 \pm 0.7$ days), moved an average of 1.03 ± 0.3 km from their natal nests, and remained at recipient nests for an average of 125.7 ± 98.3 h. The remaining four fledglings switched nests more than two weeks after fledging (late season, $\bar{x} = 20.7 \pm 4.7$ days), moved an average of 2.8 ± 1.4 km, and remained in recipient nests an average of 54 ± 34.4 h (Table 1). Both long-distance switches to remote nests (SL1Y and SE6; Table 1) occurred late in the season. All fledglings that switched nests shortly after fledging and remained at their recipient nests for close to 24 h or more received alloparental feeding (Table 1).

Nest switching arose consistently (5 of 6 times) from 3Y broods and infrequently (2 of 14 times) from 1Y broods (Fisher exact test, $P = 0.001$). In two cases, nests produced two switchers (both 3Y broods). The 3Y brood that did not produce a switcher only fledged one bird due to nestling mortality. Switchers from 3Y broods consistently moved into broods smaller than their natal broods, whereas single young moved into broods of the same or undeterminable size (Mann-Whitney test, $S = 10.5$, $P = 0.03$; Table 1). Switching events among unmarked but monitored natural broods similarly involved movement from 2Y or 3Y broods into broods where adults were still feeding dependent young.

Mean interest distances and nearest-neighbor distances were similar between nest platforms that produced switchers and those that did not (Table 2). The number of potential recipient nests (occupied platforms) within a 2-km radius of each brood did not vary significantly around nests that produced switchers versus those that did not (Table 2), nor was the number of potential recipient nests within a 2-km radius correlated with the number of switchers produced by a brood (no switchers, $\bar{x} = 5.5 \pm 0.45$ nests, $n = 14$; one switcher, $\bar{x} = 5.8 \pm 0.8$ nests, $n = 5$; two switchers $\bar{x} = 5.0 \pm 3.0$ nests, $n = 2$; univariate $F = 0.02$, $df = 1$ and 19 , $P = 0.9$). Platform densities ($G = 0.34$, $df = 2$, $P = 0.85$) and platform occupancy ($G = 2.90$, $df = 5$, $P = 0.72$) were roughly equivalent in each of the three local nesting areas that we monitored.

The perching behavior of fledglings from 1Y broods differed from that of fledglings from 3Y broods in only one respect: single fledglings explored more sites that were unused by other Ospreys during the breeding season than did 3Y groups. Singleton fledglings and sibling groups did not differ significantly in the number of days postfledging to first perching away from the nest, the number of perches used per individual, or the number of perches used per brood (Table 3). The number of post-fledging observations of each juvenile did not affect the significance of any of the above results.

Individuals in 1Y broods tended to receive more

TABLE 2. Factors around Osprey nests expected to affect the occurrence of switching if switching results from simple random movements of fledglings from nests. Values are $\bar{x} \pm SE$; Z-scores and P-values are from Mann-Whitney tests comparing nests that produced switchers with nests that did not produce switchers.

Factor	Switchers ($n = 7$)	No switchers ($n = 13$)	Z	P
Interest distance (km)	0.07 ± 0.52	0.30 ± 0.07	1.15	0.25
Nearest-neighbor distance (km)	0.04 ± 0.10	0.60 ± 0.08	-0.93	0.25
No. potential recipients (nests)	5.57 ± 0.86	5.50 ± 0.45	0.27	0.78
No. vacant sites (platforms)	4.57 ± 0.86	5.85 ± 0.55	-1.22	0.22

TABLE 3. Attributes of Osprey fledglings from 1Y (rarely switch) and 3Y (usually switch) broods (values are $\bar{x} \pm SE$). Attributes expected to be associated with increased switching from 3Y versus 1Y broods are separated into those consistent with the random-movements or the deterministic model.

Fledgling behavior	1Y broods	3Y broods	F	P
Random-movements model (df = 1 and 18)				
No. novel sites used	2.15 \pm 1.40	0.93 \pm 0.96	4.83	0.04
Total no. perches used per individual	3.29 \pm 1.53	3.56 \pm 1.29	0.05	0.84
No. days postfledging to first perch	0.07 \pm 0.52	0.94 \pm 1.34	2.41	0.14
Total no. perches used per brood	4.57 \pm 0.86	3.56 \pm 1.47	0.43	0.52
Deterministic model (df = 1 and 16)				
No. prey deliveries per observation	1.30 \pm 0.13	2.63 \pm 0.68	7.82	0.005*
Per capita provisioning ^a	1.30 \pm 0.13	0.88 \pm 0.22	3.14	0.05
Individual mean intake ^b	137.5 \pm 27.8	78.0 \pm 8.7	1.37	0.12
Average daily minimum intake ^b	78.9 \pm 27.2	29.7 \pm 12.5	3.56	0.004*
Variance in food intake ^b	60.2 \pm 30.1	50.1 \pm 5.3	0.9	0.18

* $P < 0.01$ (Bonferroni adjusted).

^a Number of feeding visits per individual.

^b Number of bites per observation (see Methods).

food than those in 3Y broods (Table 3). Small sample sizes precluded statistical significance in many cases, but the average daily food intake level in 3Y broods was roughly equivalent to the minimum in 1Y broods. Variance in food intake did not differ significantly with brood size (Table 3).

The dominance rank of nestlings that subsequently switched nests after fledging was significantly lower than that of nestlings that did not subsequently switch nests (Wilcoxon test, $S = -7.5$, $P = 0.03$). This difference in social status did not affect food intake regardless of brood size (MANOVA, $F = 0.09$, $df = 4$ and 20 , $P = 0.98$).

Manipulation of brood size did not significantly affect prey delivery rates (univariate $F = 0.72$, $df = 1$ and 17 , $P = 0.40$) or switching frequencies (Fisher exact test, $P = 0.52$), nor did translocation of a nestling to a new nest increase its likelihood of switching above that of birds that were not translocated (Fisher exact test, $P = 1.00$).

Discussion.—We found evidence of both energetic and social influences on nest switching in juvenile Ospreys. Per capita parental provisioning resulted in lower levels of food availability within 3Y broods, and switching was mostly limited to 3Y broods. Within 3Y broods, no dominant siblings switched nests, yet high rank did not appear to bias access to food in favor of dominant individuals (Gilson 1996). Instead, subtle competition among brood mates may motivate switching by subordinates early in the postfledging period, or dominant nestlings may be able to avoid energetically costly food contests (Mock et al. 1990). The two episodes of nest switching by single fledglings cannot be explained by social factors. However, both singletons that switched nests received suboptimal feeding during the early nestling period.

We observed two distinct types of switching

events: those occurring shortly after fledging, and those occurring just prior to dispersal. Switches that arose within one week of fledging involved moves of 1.5 km or less and usually (3 of 5) resulted in switchers being fed by adults at the recipient nest. All early switchers that received food remained at recipient nests overnight. Ospreys that switched nests later than one week after fledging ($n = 2$) did not receive alloparental feeding. Based on the behavior of switchers, we interpret the two types of switching events of Ospreys as follows. Early switchers are motivated by subordination and suboptimal food intake; they switch to small broods and remain at recipient nests long enough to secure food. Late switchers are not actively seeking to increase their food intake. Rather, they are simply initiating normal dispersal movements.

Patterns of use of the postfledging area fail to support the random-movements hypothesis. Single fledglings explored more novel perches, yet were less likely to switch nests than were fledglings from sibling groups. Switchers had neither more opportunities to switch (in the form of more neighbors or closer occupied nests) nor fewer alternate perches that might have forced them to visit occupied nests.

Four lines of evidence suggest that switching was not an artifact of experimental manipulation. First, one of the two 1Y switchers received no manipulation and only minimal handling as a nestling. Second, five successful switches and three attempts at switching were made by fledglings from unmarked (hence unmanipulated) broods. Third, translocated nestlings were not more likely to become switchers. Last, controlling for manipulation of brood size did not reduce error in statistical testing.

Switching at different times of the nesting cycle may have different explanations. For fledglings in the early stages of dispersal, arrival at and toleration

in a recipient nest appears to be a fortunate accident for the switcher, although potentially a maladaptive reproductive error for the host pair. For subordinate siblings and single nestlings with low food intake prior to fledging, nest switching with alloparental feeding early in the postfledging period may be an effective behavioral tactic through which they can increase food intake prior to dispersal. Variable food availability, low aggression, and poor or absent discrimination against foreign juveniles make nest switching a low-risk and potentially adaptive behavioral tactic for juvenile Ospreys.

Acknowledgments.—This research was funded by grants from the Hawk Mountain-Zeiss Raptor Research Award, the International Osprey Foundation, the Idaho Department of Fish and Game's Nongame Program, and the Raptor Research Center at Boise State University. We thank M. J. Bechard, J. C. Munger, and N. J. Clum for guidance; S. Gossett, J. Rohlman, J. Messerli, W. Seladcek, J. Somerton, H. Somerton, and C. Somerton for technical assistance; and G. Chase, K. Stieglitz, S. Canniff, A. Lani, and D. Sellers for field assistance. A. Poole and T. C. Edwards provided valuable comments on the manuscript.

LITERATURE CITED

- BUSTAMANTE, J., AND F. HIRALDO. 1989. Adoption of fledglings by Black and Red kites. *Animal Behaviour* 39:804–807.
- DONÁZAR, J. A., AND O. CEBALLOS. 1989. Acquisition of food by fledgling Egyptian Vultures *Neophron percnopterus* by nest-switching and acceptance by foster adults. *Ibis* 132:603–607.
- FERNANDEZ, J., AND G. FERNANDEZ. 1977. Some instant benefits and long range hopes from color-saturation banding of Ospreys. Pages 89–94 in *Transactions of the North American Osprey Conference* (J. C. Ogden, Ed.). United States National Park Service, Washington, D.C.
- FORBES, L. S. 1991. Hunger and food allocation among nestlings of facultatively siblicidal Ospreys. *Behavioral Ecology and Sociobiology* 29: 189–195.
- GILSON, L. N. 1996. Behavioral flexibility in juvenile Ospreys. M.S. thesis, Boise State University, Boise, Idaho.
- GONZÁLEZ, J. L., B. HEREDIA, L. M. GONZÁLEZ, AND J. C. ALONSO. 1986. Adoption of a juvenile by breeding Spanish Imperial Eagles during the postfledging period. *Raptor Research* 20:77–78.
- JUDGE, D. S. 1981. Productivity and provisioning behavior of Ospreys (*Pandion haliaetus*) in the Gulf of California. M.S. thesis, University of California, Davis.
- KENWARD, R. E., V. MARCSTRÖM, AND M. KARLBOM. 1993. Post-nestling behaviour in Goshawks, *Accipiter gentilis*: II. Sex differences in sociality and nest-switching. *Animal Behaviour* 46:371–378.
- MOCK, D. W., H. DRUMMOND, AND C. H. STINSON. 1990. Avian siblicide. *American Scientist* 78:438–449.
- NEWTON, I. 1986. *The Sparrowhawk*. T & A D Poyser, Calton, United Kingdom.
- POOLE, A. 1982. Breeding Ospreys feed fledglings that are not their own. *Auk* 99:781–783.
- SAS INSTITUTE. 1989. SAS system proprietary software release, version 6.06. SAS Institute, Inc., Cary, North Carolina.
- SPITZER, P. R. 1984. Osprey egg and nestling transfers and their value as ecological experiments and as management procedures. Pages 171–182 in *Proceedings of the Southeastern United States and Caribbean Osprey Symposium* (M. A. Westall, Ed.). The International Osprey Foundation, Sanibel, Florida.

Received 13 January 1999, accepted 2 July 1999.
Associate Editor: K. L. Bildstein