



Estimating Repeatability of Egg Size

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ABSTRACT.—Measures of repeatability have long been used to assess patterns of variation in egg size within and among females. We compared different analytical approaches for estimating repeatability of egg size of Black Brant. Separate estimates of repeatability for eggs of each clutch size and laying sequence number varied from 0.49 to 0.64. We suggest that using the averaging egg size within clutches results in underestimation of variation within females and thereby overestimates repeatability. We recommend a nested design that partitions egg-size variation within clutches, among clutches within females, and among females. We demonstrate little variation in estimates of repeatability resulting from a nested model controlling for egg laying sequence and a nested model in which we assumed laying sequence was unknown.

Egg size represents the unit of investment in a reproductive attempt for birds. Accordingly, researchers have long been interested in variation in egg size and its adaptive significance. Repeatability is a measure of the proportion of variation in a trait that is due to differences among individuals. Therefore, estimates of repeatability of egg size split the total phenotypic variation in egg size into within-individual and among-individual components. Falconer (1989) describes that partitioning of the phenotypic variance in terms of the origin of the different variance components. Variation in egg size among individuals is caused by a combination of genetic and environmental differences. Variation in egg size within an individual among years is caused by temporary environmental differences between reproductive attempts. Falconer (1989) goes on to demonstrate that estimates of repeatability are useful in the context of quantitative genetics because they set upper limits to levels of heritable variation.

Falconer (1989) states that estimates of repeatability can be based on measures of a characteristic that are

repeated in either time or space. Following Falconer's (1989) descriptions, egg size is repeated in both time and space—where time refers to different nesting attempts and space refers to eggs within a specific nesting attempt (i.e. clutch). In many cases researchers estimating repeatability of egg size use the average egg size within clutches (e.g. Lessells et al. 1989, Flint and Sedinger 1992, Flint and Grand 1996). However, that approach ignores some of the phenotypic variation in egg size within individuals (e.g. within clutches) and may have been used because researchers were uncertain how to deal with multiple measurements within clutches statistically. Other researchers have used a nested design to partition variance among females, within females among years, and within females within years (i.e. clutches) (LeBlanc 1987, Erikstad et al. 1998, Flint and Grand 1999).

In this paper, we compare those two approaches in terms of estimates of repeatability. We decompose each estimate into its variance components and discuss each estimate in the context of quantitative genetics. We also discuss those estimates relative to the assumptions of repeatability analyses. Finally, we recommend approaches for estimating repeatability of egg size given specific data sets.

Methods.—This study was conducted at the Tutakoke River Black Brant (*Branta bernicla nigricans*) colony along the outer coastal fringe of the Yukon-Kuskokwim Delta from 1987–1997. Breeding Black Brant have been banded at that site since 1986, providing a large sample of identifiable females on which to measure repeatability. Methods of nest searching, measuring of eggs, and estimation of egg volume have been described by Flint and Sedinger (1992). Estimation of repeatability requires multiple measurements of individuals among years, and that large data set allowed partitioning to many different levels (i.e. specific clutch size and egg sequence numbers). In each analyses, we deleted individuals for which we did not have multiple measurements; therefore, sample sizes vary for each analyses. Further, we restricted our analyses to clutches of 3, 4,

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TABLE 1. Estimated repeatability of egg size by clutch size and egg sequence number for Black Brant nesting on the Yukon-Kuskokwim Delta, Alaska.

Clutch size	Egg-sequence number				
	1	2	3	4	5
3	0.6394 (96:209) ^a	0.5544 (95:204)	0.6069 (91:197)		
4	0.5482 (354:814)	0.5371 (346:804)	0.5505 (353:815)	0.5287 (349:805)	
5	0.5532 (280:674)	0.5021 (280:675)	0.5698 (271:655)	0.5308 (277:671)	0.4929 (267:642)

^a Sample sizes for each estimate are given in parentheses as: (number of females:number of eggs).

or 5 eggs because those are the most common clutch sizes. Clutches <3 and >5, are likely the result of partial nest predation and intraspecific nest parasitism, respectively. By excluding those clutches, we attempted to reduce the possibility that either partial predation or intraspecific nest parasitism influence our determination of clutch size, egg sequence number, or both.

Analyses.—We used SAS (PROC NESTED) to estimate the true variance components for each data set (SAS Institute 1990). Therefore, consistent with Lessells and Boag (1987), our estimates of repeatability were based on variance components extracted from mean squares of the various models. We performed four main analyses. First, to control for egg-size variation among clutch sizes and due to egg-sequence number, and to avoid statistical problems associated with multiple measures within females, we partitioned the data set by clutch size and egg sequence number. We then estimated the repeatability for each egg-sequence number within clutch sizes using a series of one-way ANOVA models. Second, we replicated previous studies and calculated the average egg size for each clutch and estimated the repeatability of average egg size from multiple samples across years using a one-way ANOVA. Third, we used the complete data set and partitioned the variance among females, within females among years, and within clutches using a nested ANOVA design. Finally, we controlled for the combination of clutch size and egg-sequence number, then partitioned the remaining variance within and among females using a nested ANOVA.

To interpret the differences among those approaches to estimating repeatability estimates, we must examine the contribution of the different variance components. From Falconer (1989), we use the following: V_p = phenotypic variation at the population level, V_g = variation in egg size due to genetic differences among individuals, V_{eg} = general environmental variation among individuals arising from permanent or nonlocalized circumstances, and V_{es} = special environmental variation within individuals arising from annual variation in circumstances. As we noted above, egg size within individuals is repeated on several scales (i.e. among years and within

clutches). Thus, we add the following: V_c = variation within clutches. Based on those definitions, when using the approach of averaging egg size within clutches or when restricting analyses to a specific egg-sequence number from a specific clutch size:

$$V_p = V_g + V_{eg} + V_{es} \quad (1)$$

Alternatively, when using a nested design:

$$V_p = V_g + V_{eg} + V_{es} + V_c \quad (2)$$

Given these definitions, repeatability as defined by Falconer (1989) is:

$$r = (V_g + V_{eg}) / V_p \quad (3)$$

Results and discussion.—Estimates of repeatability of egg size vary considerably depending on how they are calculated (Tables 1 and 2). Using Equations 1 and 2, it is clear that estimates of repeatability based on the nested design will always be less than or equal to those based on average egg size within clutches because of the additional term (V_c) in the denominator of Equation 3. In cases where there is no variation in egg size within clutches (i.e. $V_c = 0$), estimates of repeatability based on average egg size and the nested design will be equal. Thus, ignoring within-clutch variation in egg size, if it exists, inflates estimates of repeatability. In addition, using the average of multiple measurements will inflate the estimated repeatability because the mean of two or more measures has a higher heritability than does a single measurement (Falconer 1989). Therefore, the use of average egg size to estimate repeatability will result in estimates that are biased high. Finally, estimates of repeatability rely on the assumption that different measurements reflect what is genetically the same character (Falconer 1989). All eggs in a clutch originate from the same female, and in that sense there is no genetic variation in egg size within clutches. However, in Black Brant, egg size varies with the combination of clutch size and egg-laying sequence (Flint and Sedinger 1992) and a similar pattern of egg-size variation within clutches has been shown for other species of geese (Cooper 1978, Leblanc 1987, Owen and West 1988, Robertson and Cooke 1993, Williams et al. 1993, Cooke et al. 1995). Additionally, intraclutch patterns of egg size have been shown for many species of birds with altricial

TABLE 2. Partitioning phenotypic variance in egg size of Black Brant nesting on the Yukon-Kuskokwim Delta, Alaska within and among females using ANOVA.

Method of analysis ^a	Proportion of phenotypic variance		
	Among females ^b	Within females among years	Within clutches
One-way ANOVA based on average egg size per clutch	0.7099	0.2901	
Nested ANOVA—assuming egg sequence numbers unknown	0.5118	0.1180	0.3702
Nested ANOVA—controlling for clutch size and egg sequence number	0.5584		

^a Sample size equals 12,506 eggs from 1,246 females.

^b Repeatability.

young (Lack 1968, Slagsvold et al. 1984). Those patterns, repeated across many species, raise the possibility that intraclutch egg-size variation may be adaptive (Lack 1968, Slagsvold et al. 1984, Williams et al. 1993, Flint et al. 1994, Williams 1994, Erikstad et al. 1998). If so, the level and pattern of variation in egg size within clutches may be genetically determined. Thus, estimating the repeatability by averaging egg size within clutches and using a one-way ANOVA would result in averaging across characters that may not be the same genetic character. Under those conditions, Falconer (1989:141) states that "repeatability becomes a somewhat vague concept, without precise meaning in relation to the components of variance." The genetic basis and genetic influence on intraclutch egg-size variation deserves further study. Therefore, we caution researchers to temper inferences drawn from estimates of repeatability that are based on mean egg size within clutches because those estimates are likely biased.

When we partitioned our data and estimated repeatability of egg size by sequence number, there was little difference in the estimated repeatability among clutch sizes or egg sequence numbers. Most of the variation among those partitioned estimates of repeatability was likely caused by sampling error. Clearly those estimates are free from bias associated with averaging multiple measurements. Further, those estimates would not be biased if all eggs within a clutch are not genetically the same character. Therefore, we conclude that the true value of egg size repeatability for Black Brant lies between 0.49 and 0.64. However, for comparative purposes, it is difficult to have a separate estimate of repeatability for each egg sequence number in each clutch size. Also, that approach can only be used if egg-laying sequence is known. For many species of birds, determination of laying sequence in field studies is not practical. The estimated repeatabilities from the two nested ANOVA (Table 2) fall within the range predicted from the individual estimates by clutch size and egg-sequence number (Table 1). We believe either approach correctly models the multiple measurements within clutches and results in a good approximation of repeatability. We suggest future studies should examine patterns of egg-size variation with egg sequence when possible. If consistent patterns of egg-size variation ex-

ist, then estimates of egg size repeatability could control for egg sequence and partition the remaining variance within and among females. If the pattern of variation with egg-sequence number varies among clutch sizes (e.g. as it does for Black Brant), then estimates of repeatability should control for the combination of clutch size and egg sequence. In the absence of data on egg size by laying sequence, we suggest the nested design partitioning variance among females, within females among years, and within clutches is most appropriate for estimating repeatability. It is useful to note that the proportion of variance attributed to differences among females (i.e. repeatability) is similar in both models. Thus, the nested design without egg-sequence numbers could be used in all cases and gives the clearest picture regarding the distribution of the variance within females.

Estimation of repeatability from large data sets can be computationally tedious (Lessells and Boag 1987), particularly if the design is unbalanced. Previous researchers have used program SAS (PROC NESTED; SAS Institute 1990) to partition the phenotypic variation in egg size (Erikstad et al. 1998, Flint and Grand 1999). That procedure is useful because it calculates the actual variance components in addition to the mean square errors (Lessells and Boag 1987). However, it is important to realize that nested ANOVA is a hierarchical analysis and results will vary depending on the order in which variables are listed in the model (Sokal and Rohlf 1981). Erikstad et al. (1998) examined variation in egg size with a nested model in the following order: year, females, clutch size, egg sequence, error. It is clear that variation within clutches (i.e. egg-sequence number) must be considered as nested within clutch sizes; however, clutch sizes should not be nested within females. Therefore, it is essential to consider the hierarchical structure of the variance when using a nested ANOVA. We recommend the following hierarchical orders (1) when egg sequence is known: clutch size, egg sequence number, female; (2) when egg sequence is unknown: female, nest attempt.

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LITERATURE CITED

- COOKE, F., R. F. ROCKWELL, AND D. B. LANK. 1995. The Snow Geese of La Pèrouse Bay: Natural Selection in the Wild. Oxford University Press, New York.
- COOPER, J. A. 1978. The history and breeding biology of the Canada Geese of Marshy Point, Manitoba. Wildlife Monographs, no. 61.
- ERIKSTAD, K. E., T. TVERAA, AND J. O. BUSTNES. 1998. Significance of intraclutch egg-size variation in Common Eider: The role of egg size and quality of ducklings. *Journal of Avian Biology* 29:3-9.
- FALCONER, D. S. 1989. Introduction to Quantitative Genetics, 3rd ed. John Wiley and Sons, New York.
- FLINT, P. L., AND J. B. GRAND. 1996. Variation in egg size of the Northern Pintail. *Condor* 98:162-165.
- FLINT, P. L., AND J. B. GRAND. 1999. Patterns of variation in size and composition of Greater Scaup eggs: Are they related? *Wilson Bulletin* 111:465-471.
- FLINT, P. L., M. S. LINDBERG, M. C. MACCLUSKIE, AND J. S. SEDINGER. 1994. The adaptive significance of hatching synchrony of waterfowl eggs. *Wildfowl* 45:248-254.
- FLINT, P. L., AND J. S. SEDINGER. 1992. Reproductive implications of egg size variation in the Black Brant. *Auk* 109:896-903.
- LACK, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen, London.
- LEBLANC, Y. 1987. Intraclutch variation in egg size of Canada Geese. *Canadian Journal of Zoology* 56:3044-3047.
- LESSELLS, C. M., AND P. T. BOAG. 1987. Unrepeatable repeatabilities: A common mistake. *Auk* 104:116-121.
- LESSELLS, C. M., F. COOKE, AND R. F. ROCKWELL. 1989. Is there a trade-off between egg weight and clutch size in Lesser Snow Geese (*Anser c. caerulescens*)? *Journal of Evolutionary Biology* 2:457-472.
- OWEN, M., AND J. WEST. 1988. Variation in egg composition in semi-captive Barnacle Geese. *Ornis Scandinavica* 19:58-62.
- ROBERTSON, G. J., AND F. COOKE. 1993. Intraclutch egg-size variation and hatching success in the Common Eider. *Canadian Journal of Zoology* 71:544-549.
- SAS INSTITUTE. 1990. SAS/STAT User's Guide, version 6. SAS Institute Inc., Cary, North Carolina.
- SLAGSVOLD, T., J. SANDVIK, G. ROFSTAD, Ö. LORENTSEN, AND M. HUSBY. 1984. On the adaptive value of intraclutch egg-size variation in birds. *Auk* 101:685-697.
- SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd ed. W. H. Freeman and Company, New York.
- WILLIAMS, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: Effects on offspring fitness. *Biological Reviews of the Cambridge Philosophical Society* 68:35-59.
- WILLIAMS, T. D., D. B. LANK, AND F. COOKE. 1993. Is intraclutch egg-size variation in the Lesser Snow Goose adaptive? *Oikos* 67:250-256.

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Effect of Investigator Disturbance on Nest Attendance and Egg Predation in Eurasian Oystercatchers

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ABSTRACT.—Eurasian Oystercatchers (*Haematopus ostralegus*) breeding on the salt marsh of Schiermonnikoog (Dutch Wadden Sea) lose many eggs to pred-

ators, mainly Herring (*Larus argentatus*) and Mew gulls (*L. canus*). We estimated that the probability for an egg to survive from laying until hatching was 69%. Daily egg mortality was higher during the laying period than during the incubation period. When researchers were present in the study area, oystercatchers spent more time at greater distances from the nest. We investigated whether human disturbance resulted in more eggs being lost to predators. Two experimental areas were in turn visited at high and at low frequency. From a preliminary analysis, we estimated higher daily egg mortality rates when nests were checked three times per day instead of once every oth-

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er day. However, high-frequency nest checks provided more information on newly laid and lost eggs, especially during the laying period. After correcting for that extra information (by simply deleting it), the egg mortality rates were no longer different. We conclude that human disturbance did not increase egg loss, rather egg mortality rates were underestimated when nests were checked only once per two days.

Because many life-history characters evolve under the influence of high predation pressure, it is important to know the level of nest predation in natural populations. Unfortunately, it is not always easy to obtain reliable estimates of predation rates. Predation events are seldom witnessed, and visiting nests to check the contents necessarily results in disturbance of the individuals being studied. Moreover, investigator disturbance may increase the probability of nest predation (Lenington 1979). Predators may be attracted by packed vegetation around the nest (Esler and Grand 1993), human scent (Whelan et al. 1994), or nest markers (Picozzi 1975, Yahner and Wright 1985). Human disturbance may also reduce nest attendance or enhance conspicuous behavior of the parents. Some studies have shown that predators learn to follow biologists in the field (e.g. MacInnes and Misra 1972, Götmark and Åhlund 1984). Other studies found no effect of human disturbance on nest predation (e.g. Seding 1990, Hannon et al. 1993). Obviously, it is of primary importance to find out if research activities influence nesting success of birds under study and if predation rates are affected by visiting nests.

We studied egg predation in a population of Eurasian Oystercatchers (*Haematopus ostralegus*). Oystercatchers typically experience high nest-predation rates (Harris 1967). That might be because they forage on intertidal areas, away from the breeding territory. Ens (1991) suggested that high predation rates during egg laying could be due to the first eggs being left unattended when the male escorts the female on feeding trips to prevent rival males from fertilizing subsequent eggs in the clutch. Thus, high egg-predation rates could be due to a trade-off between two conflicting activities: nest attendance and, for example, foraging or mate guarding.

The aim of this study was to find out if high levels of egg loss were due to limited nest attendance during the laying period or research activities in the study area, or both. We estimated the probability that oystercatcher eggs disappeared from the nest during different stages of the nesting cycle. In addition, we estimated egg-predation rates in artificial nests unattended by parents. If nest attendance reduces the probability of egg loss, we expect to find higher egg mortality rates in those nests as compared to natural nests, where parents are present. We further studied nest attendance in situations in which researchers were either present or absent in the direct vicinity of the nest. To find out if human

disturbance increased egg predation rates, we compared the rate at which eggs disappeared from two experimental areas that were in turn subjected to different levels of disturbance.

Study Area and Methods.—We studied Eurasian Oystercatchers breeding on the saltmarsh of Schiermonnikoog, an island in the Dutch Wadden Sea. Since 1985, we marked birds with color rings and measured their reproductive success as part of a long-term population study (Ens et al. 1992, Heg 1999). Occasional observations had indicated that oystercatchers in our study area lose many eggs to Mew (*Larus canus*) and Herring (*L. argentatus*) gulls. In 1990, we randomly selected 20 pairs to study nest attendance. Those pairs were observed from a blind every other day from laying until the first egg hatched, or until 6 July 1990 when all eggs and chicks were washed away by a catastrophic flood accompanied by bad weather. The observations lasted for one 1 h and started ~10 min after entering the blind when disturbed birds had settled down. With the aid of an electronic event recorder, we continuously monitored distance of the male and female from the nest. We analysed amount of time both parents spent within four distance classes: 0–1, 1–10, 10–50, >50 m. In addition, we recorded how long both parents spent incubating the eggs. The main cause of disturbance in the study area was the presence of colleagues checking nests or walking to or from a blind. We coded our observations as “disturbed” as long as people were present within a distance of 150 m from the nest and compared nest attendance during disturbed and undisturbed time intervals.

To estimate egg-predation rates, we searched the main study area (area A, Heg 1999) every other day to find new nests and to check the contents of nests already known to us. Some nests were found after the start of incubation. For those nests, the laying date was calculated using the date of hatching and assuming an incubation period of 27 days (Keighley and Buxton 1948). If the nest was found after laying and failed before hatching, or if the outcome was unknown, we assumed that we had discovered it one day after the last egg had been laid.

To estimate predation rates of eggs unattended by parents, we used oystercatcher eggs that became available after an egg removal experiment (Ens 1992). Those eggs were laid out on the salt marsh in locations that seemed suitable nest sites to human observers. We created four nests with three eggs each on five subsequent days (19 to 23 May) and recorded egg losses after 2 h of exposure.

The effect of human disturbance on egg predation was tested in two areas adjacent to the main study area (areas C and D, Heg 1999). In those areas, the birds were not ringed and no other research activities took place. Nests were checked by one observer who walked through the area in linear transects that were 5 to 10 m apart. The duration of one visit was

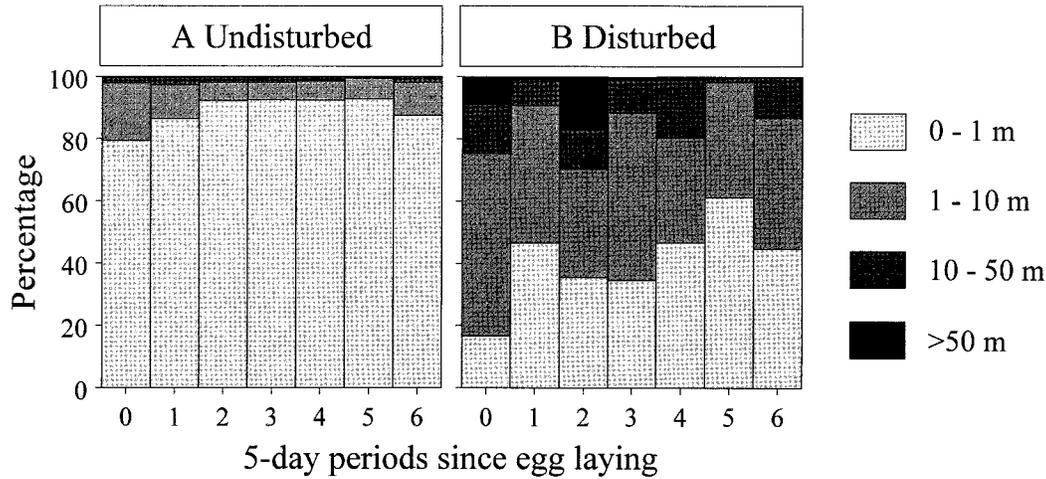


FIG. 1. The percentage of time the closest parent spent at different distances from the nest plotted for different stages of the nesting cycle. The stage of the nesting cycle is expressed as 5 day periods since egg laying (0 = egg laying). (A) undisturbed observations and (B) disturbed situations in which researchers were present within a distance of 150 m of the nest.

45 to 60 min. Each week, one area was subject to a high disturbance treatment whereas the other was subject to a low disturbance treatment. The pattern was reversed every other week until week eight when the experiment ended. The high disturbance treatment consisted of four days of intense nest inspection in which the nests were checked three times daily (morning, afternoon, and evening). After four days, one further nest check was made before the next week started. In the low-disturbance treatment, the nests were checked once every other day. Egg mortality rates were calculated over the interval of four days of thrice-daily nest checks and compared to egg mortality rates during periods of low visitation frequency.

Laying date and clutch size in the different areas were compared using generalised linear models with normal errors and "identity" link function (Crawley 1993), and *P*-values were calculated with *F*-tests. We analysed frequencies with the *G*-test for goodness-of-fit for single classification, and applied Williams' correction to reduce type I error (Sokal and Rohlf 1981). Daily egg mortality rates (*m*) were calculated by dividing number of eggs lost by total number of days eggs were exposed to predation (Mayfield 1961, 1975). Standard errors and significance levels were calculated according to Johnson (1979). We divided the incubation period into 5 day periods to analyse nest attendance and egg mortality in relation to the stage of the nesting cycle. Data were analysed using SAS (SAS Institute 1990), all tests are two-tailed, and means are reported ± 1 SE.

Results.—Nest attendance was high throughout the laying and incubation period. More than 95% of the time at least one parent was present within a dis-

tance of 50 m from the nest (Fig. 1A). The observations on incubation behavior showed that during egg laying the parents spent 78% of the time actually sitting on the eggs. The time spent close to the nest decreased dramatically when researchers were present in the study area (Fig. 1B).

In the main study area, a total of 38 clutches were laid between 4 April and 29 June 1990. The mean clutch size was 2.6 ± 0.2 eggs. In total, 21 eggs disappeared in 17 predation events. That means that usually one egg was taken at a time. We compared the daily egg mortality rates in nests with and without previous predation to find out if predators repeatedly visited the same nest. Those values were not significantly different ($m_{\text{previous predation}} = 0.031$, $m_{\text{no previous predation}} = 0.021$, $t = 0.4$, $df = 15$, $P = 0.7$) and the probability of committing type II error was low ($\beta = 0.10$). We conclude that nests preyed upon in the past were not more likely to be preyed upon in the future. Although that cannot firmly prove that eggs disappeared independently from each other, we use egg-predation rates rather than nest-predation rates. Both measures gave the same result unless otherwise stated.

The probability of an egg disappearing from the clutch decreased with the stage of the nesting cycle (Fig. 2). Daily egg mortality was significantly higher in the laying period than in the incubation period ($m_{\text{laying}} = 0.035 \pm 0.012$, $m_{\text{incubation}} = 0.007 \pm 0.002$, $t = 2.4$, $df = 19$, $P = 0.03$). The same was found for nest-predation rates, although the difference was not significant ($P = 0.14$). However, a decline in egg loss from laying to hatching could be confounded with calendar date, because younger nests tended to be found earlier in the breeding season. We split the data set into clutches laid before and after 1 May

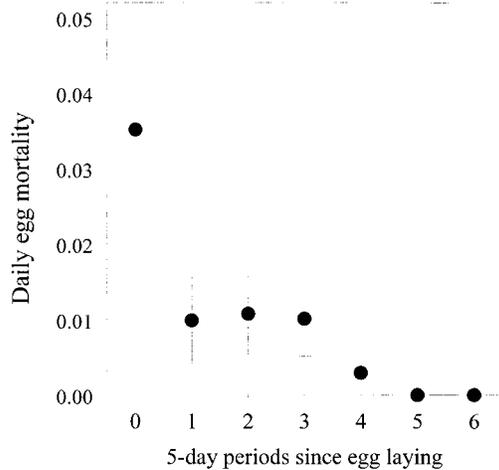


FIG. 2. Daily egg-mortality rates (\pm SE) in the non-experimental area plotted against the stage of the nesting cycle. The stage of the nestling cycle is expressed as 5 day periods since egg laying (0 = egg laying).

1990. We found no differences in daily egg mortality between the early and the late groups either during laying ($m_{\text{early}} = 0.034$, $m_{\text{late}} = 0.033$, $t = 0.04$, $df = 7$, $P = 0.1$) or during incubation ($m_{\text{early}} = 0.005$, $m_{\text{late}} = 0.008$, $t = 0.7$, $df = 10$, $P = 0.5$). The overall probability for an egg to survive a 5 day laying period together with the 27 day incubation period was $(1 - 0.035)^5 \times (1 - 0.007)^{27} = 69\%$.

Eggs in artificial nests were more likely to disappear than eggs from natural nests. Altogether 18 unattended eggs disappeared, which equals to a mortality rate of 0.15 ± 0.033 eggs per hour. Eggs in artificial clutches were thus approximately 60 times more likely to disappear than eggs in active nests, suggesting that nest attendance lowered the probability of egg predation.

The two experimental areas that were periodically subject to high visitation frequency had 48 and 50 clutches, which did not differ in mean laying date ($F = 0.02$, $df = 1$, $P = 0.89$) or clutch size ($F = 0.87$, $df = 1$, $P = 0.35$). Also, egg-predation rates in the two experimental areas were not significantly different from each other ($m = 0.032$ vs. $m = 0.022$, $t = 1.76$,

$df = 94$, $P = 0.08$). Clutch sizes of one tended to be more frequent in the two periodically disturbed areas as compared to the main study area (16% in the main study area vs. 31% in the experimental areas, $G_{\text{adj}} = 3.3$, $df = 1$, $P = 0.07$).

We found that daily egg mortality rates were higher when nests were checked three times daily compared to once every two days. That difference was significant for the laying period, but not for the incubation period (Table 1). That suggests that human disturbance increased the probability that eggs were taken by predators early in the nesting cycle. However, not only did visiting the study area cause disturbance, it also increased our knowledge about newly laid and lost eggs. During a disturbed block of four days, the area was checked as many as 12 times. We recalculated the daily egg mortality rates by taking into account only two of those visits to make the search effort, but not the actual disturbance, equal to that in control blocks, and the difference disappeared (Table 1). From freshly laid second, third, and fourth eggs during the high-frequency nest checks, we estimated that oystercatchers produced eggs at 30.5 ± 1.6 h intervals. Thus, inspecting the nests every other day was not enough to find all eggs that were laid. We conclude that human disturbance did not increase predation rates, rather we found more eggs before they were lost to predators when we visited the study area more frequently.

Discussion.—Our results show that many oystercatcher eggs at our study site were lost before hatching. That is in agreement with other studies in which egg predation by gulls was a major cause of low breeding success in this species (e.g. Heppleston 1972, Briggs 1984, Beinetma and Müskens 1987). Harris and Wanless (1997) followed an oystercatcher population after the start of a large-scale gull control program. Although the breeding success remained low, number of breeding pairs increased markedly, suggesting that the absence of gulls made the nesting area more attractive for oystercatchers.

Predation rates were highest during the laying period, and eggs were lost despite the presence of at least one parent within 50 m of the nest most of the time. Nevertheless, nest attendance seemed to reduce

TABLE 1. Daily egg-mortality rates (\pm SE) on occasions when clutches were checked three times per day (high-level disturbance) and when clutches were checked once every two days (low-level disturbance). In the right-hand column, daily egg mortality rates are corrected for increased searching effort due to disturbance by ignoring the information on newly laid and lost eggs obtained during extra nest checks. *P*-values indicate significance levels for the comparison of high-level disturbance with low-level disturbance.

	Low	High	High (after correction)
Laying	0.0618 \pm 0.0128	0.2103 \pm 0.0483 ($P = 0.004$)	0.0708 \pm 0.0258 ($P = 0.8$)
Incubation	0.0160 \pm 0.0026	0.0275 \pm 0.0058 ($P = 0.08$)	0.0225 \pm 0.0052 ($P = 0.3$)

probability of an egg being lost because, assuming that clutches created by us mimicked real nests, we found higher predation rates in artificial nests than in nests where parents were present. Moreover, during laying, oystercatchers spent less time actually sitting on the eggs as opposed to being present in the territory. However, the fact that oystercatcher eggs were being incubated for no less than 78% of the time already before the clutch was complete could in itself be an adaptation to overcome high predation rates as suggested for pheasants (*Phasianus colchicus*) by Persson and Göransson (1999).

When people were present in the study area, parents spent more time at larger distances from the nest. However, when comparing egg predation for high and low levels of disturbance within the experimental areas, we found that the apparent difference in egg-mortality rates was due to extra information rather than to disturbance resulting from the extra nest checks. For the incubation period, that difference was less pronounced ($P = 0.08$, Table 1). That is not surprising, because at that time the clutches were complete and no additional information was gathered by checking the nests more frequently.

Several studies tested for an effect of human activity on nest predation by assigning nests to different visitation schedules, and the results are ambiguous. High visitation frequencies increased predation in some studies (e.g. Salathé 1987, Major 1990), but not in others (e.g. Willis 1973, Nichols et al. 1984, O'Grady et al. 1996). In some studies, artificial nests were used so that parental behavior was not taken into account (e.g. Esler and Grand 1993, Bayne and Hobson 1997). Other studies give the percentage of eggs or nests lost instead of Mayfield estimates (e.g. Robert and Ralph 1975). The latter will underestimate predation, unless the searching effort is high (Mayfield 1975) which, in this case, is equal to human disturbance.

After losing the first egg, oystercatchers often move to a new nest scrape to lay the remaining eggs of the clutch (Harris 1967). Also, if the complete clutch is lost early in the breeding season, they may switch to a new nest scrape and lay a replacement clutch (Ens et al. 1996). If those clutches are mistaken as first clutches, laying date and clutch size will be estimated incorrectly. Unfortunately, we can not be absolutely sure about birds moving to new nests in the experimental areas because here the birds were not ringed. However, single-egg clutches tended to be more frequent in the two periodically disturbed areas than in the main study area. Thus, searching effort may not only affect the estimation of egg-predation rates, but it may also have consequences for the determination of laying date and clutch size.

This study showed that searching effort influenced estimates of daily egg mortality. Because nest predation is a major determinant of avian reproductive success, we suggest that extra care should be taken

when interpreting the results of nesting studies with high egg-predation rates, especially during the laying period.

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LITERATURE CITED

- BAYNE, E. M., AND K. A. HOBSON. 1997. Temporal patterns of predation on artificial nests in the southern boreal forest. *Journal of Wildlife Management* 61:1227–1234.
- BEINTEMA, A. J., AND G. J. D. M. MÜSKENS. 1987. Nesting success of birds breeding in Dutch agricultural grasslands. *Journal of Applied Ecology* 24:743–758.
- BRIGGS, K. 1984. The breeding ecology of coastal and inland oystercatchers in North Lancashire. *Bird Study* 31:141–147.
- CRAWLEY, M. J. 1993. *GLIM for Ecologists*. Blackwell Scientific Publications, Oxford.
- ENS, B. J. 1991. Guarding your mate and losing the egg: An oystercatcher's dilemma. *Wader Study Group Bulletin* 61(Supplement):69–70.
- ENS, B. J. 1992. The social prisoner. Ph.D. dissertation, University of Groningen, Groningen, The Netherlands.
- ENS, B. J., K. B. BRIGGS, U. N. SAFRIEL, AND C. J. SMIT. 1996. Life history decisions during the breeding season. Pages 186–218 in *The Oystercatcher, from Individuals to Populations* (J. D. Goss-Custard, Ed.). Oxford University Press, Oxford.
- ENS, B. J., M. KERSTEN, A. BRENNINKMEIJER, AND B. J. HULSCHER. 1992. Territory quality, parental effort and reproductive success of Oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology* 61:703–715.
- ESLER, D., AND J. B. GRAND. 1993. Factors influencing depredation of artificial duck nests. *Journal of Wildlife Management* 57:244–248.
- GÖTMARK, F., AND M. ÅHLUND. 1984. Do field observers attract nest predators and influence nesting success of Common Eiders? *Journal of Wildlife Management* 48:381–387.
- HANNON, S. J., K. MARTIN, L. THOMAS, AND J. SCHIECK. 1993. Investigator disturbance and clutch predation in Willow Ptarmigan: Methods for evaluating impact. *Journal of Field Ornithology* 64:575–586.
- HARRIS, M. P. 1967. The biology of Oystercatchers *Haematopus ostralegus* on Skokholm Island, S. Wales. *Ibis* 109:180–193.

- HARRIS, M. P., AND S. WANLESS. 1997. The effect of removing large numbers of gulls *Larus* spp. on an island population of Oystercatchers *Haematopus ostralegus*: Implications for management. *Biological Conservation* 82:167–171.
- HEG, D. 1999. Life history decisions in oystercatchers. Ph.D. dissertation, University of Groningen, Groningen, The Netherlands.
- HEPPLESTON, P. B. 1972. The comparative breeding ecology of Oystercatchers (*Haematopus ostralegus*) in inland and coastal habitats. *Journal of Animal Ecology* 41:23–51.
- JOHNSON, D. H. 1979. Estimating nest success: The Mayfield method and an alternative. *Auk* 96: 651–661.
- KEIGHLEY, J., AND E. J. M. BUXTON. 1948. The incubation period of the oyster-catcher. *British Birds* 41:261–266.
- LENINGTON, S. 1979. Predators and blackbirds: The “uncertainty principle” in field biology. *Auk* 96: 190–192.
- MACINNES, C. D., AND R. K. MISRA. 1972. Predation on Canada Goose nests at McConnell River, Northwest Territories. *Journal of Wildlife Management* 36:414–422.
- MAJOR, R. E. 1990. The effect of human observers on the intensity of nest predation. *Ibis* 132:608–612.
- MAYFIELD, H. F. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255–261.
- MAYFIELD, H. F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456–466.
- NICHOLS, J. D., H. F. PERCIVAL, R. A. COON, M. J. CONROY, G. L. HENSLER, AND J. E. HINES. 1984. Observer visitation frequency and success of Mourning Dove nests: A field experiment. *Auk* 101:398–402.
- O’GRADY, D. R., D. P. HILL, AND R. M. R. BARCLAY. 1996. Nest visitation by humans does not increase predation on Chestnut-collared Longspur eggs and young. *Journal of Field Ornithology* 67: 275–280.
- PERSSON, I., AND G. GÖRANSSON. 1999. Nest attendance during egg laying in pheasants. *Animal Behaviour* 58:159–164.
- PICOZZI, N. 1975. Crow predation on marked nests. *Journal of Wildlife Management* 39:151–155.
- ROBERT, H. C., AND C. J. RALPH. 1975. Effects of human disturbance on the breeding success of gulls. *Condor* 77:495–499.
- SALATHÉ, T. 1987. Crow predation on coot eggs: Effects of investigator disturbance, nest cover and predator learning. *Ardea* 75:221–229.
- SAS INSTITUTE. 1990. SAS/STAT User’s Guide, version 6, 4th ed. SAS Institute Inc., Cary, North Carolina.
- SEDINGER, J. S. 1990. Effects of visiting Black Brant nests on egg and nest survival. *Journal of Wildlife Management* 54:437–443.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*, 2nd ed. W. H. Freeman and Company, New York.
- WHELAN, C. J., M. L. DILGER, D. ROBSON, N. HALLYN, AND S. DILGER. 1994. Effects of olfactory cues on artificial-nest experiments. *Auk* 111:945–952.
- WILLIS, E. O. 1973. Survival rates for visited and unvisited Bicolored Antbirds. *Auk* 90:263–267.
- YAHNER, R. H., AND A. L. WRIGHT. 1985. Depredation on artificial ground nests: Effects of edge and plot age. *Journal of Wildlife Management* 49:508–513.

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Nocturnal Activities of Post-breeding Wood Storks

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ABSTRACT.—Postbreeding season activities of Wood Storks (*Mycteria americana*) were examined during 24 h long observation periods at inland impoundments and a coastal roost site. Storks were

present at inland impoundments and foraged more at night there than at other times of the day. Wood Stork attendance at the coastal roost site was significantly reduced during nocturnal low tides than during daytime low tides or at either period of higher tide levels. Presumably, storks were leaving the roost to forage on fish concentrated in tidal creeks by dropping tides. Nocturnal foraging in freshwater

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TABLE 1. Average number of Wood Storks present and foraging at the Kathwood impoundments in relation to time-of-day^a.

Date	Diurnal		Crepuscular		Nocturnal	
	Total present $\bar{X} \pm SD$	No. foraging storks $\bar{X} \pm SD$	Total present $\bar{X} \pm SD$	No. foraging storks $\bar{X} \pm SD$	Total present $\bar{X} \pm SD$	No. foraging storks $\bar{X} \pm SD$
7-8 Jul 94	56 ± 9	17 ± 19	73 ± 10	35 ± 29	76 ± 2	51 ± 25
14-15 Jul 94	22 ± 13	11 ± 14	29 ± 3	14 ± 13	30 ± 3	16 ± 12
18-19 Jul 94	63 ± 5	18 ± 24	112 ± 3	52 ± 35	107 ± 9	36 ± 32
28-29 Jul 94	59 ± 48	8 ± 19	101 ± 16	10 ± 10	108 ± 4	48 ± 34
1-2 Aug 94	7 ± 6	0 ± 1	43 ± 13	1 ± 2	55 ± 9	26 ± 12
3-4 Aug 94	0 ± 0	0 ± 0	22 ± 19	2 ± 3	33 ± 16	1 ± 4
13-14 Aug 95	20 ± 19	2 ± 3	40 ± 21	8 ± 6	55 ± 2	3 ± 8
27-28 Jul 95	46 ± 13	23 ± 22	58 ± 1	27 ± 16	58 ± 0	20 ± 20
10-11 Aug 95	22 ± 42	12 ± 27	122 ± 50	30 ± 48	156 ± 2	98 ± 44
19-20 Jul 96	8 ± 10	2 ± 3	37 ± 26	12 ± 12	66 ± 4	14 ± 3
Total	28 ± 36	9 ± 28	63 ± 41	19 ± 27	75 ± 38	31 ± 37

^a Time Periods (EST): Diurnal 0800 to 1800 h; Crepuscular 0500 to 0800 h, 1800 to 2100h; Nocturnal 2100 to 0500 h.

and estuarine systems may be an advantageous strategy for the tactile-feeding storks by reducing the likelihood of their being observed by their prey and possibly by reducing competition with other wading birds. Also, some prey species in both freshwater and saltwater environments are more active nocturnally than diurnally, this increasing their likelihood of capture by nocturnal-foraging Wood Storks. In the coastal setting, low tide events (two per ~24 h) typically provide at least one "pulse" of stork prey in draining tidal creeks during the nocturnal period.

Typically, wading birds (Ciconiiformes) forage most actively near dawn and dusk and rest at midday, although night foraging has been documented for several species (Kushlan 1978). Nocturnal activities have not been examined quantitatively for most species (McNeil et al. 1993). Nocturnality, including foraging, has been reported anecdotally for Wood Storks (*Mycteria americana*) (Bent 1926, Coulter et al. 1987, Kahl 1964). Nocturnal foraging is a likely strategy for Wood Storks due to their tactile feeding that does not require them to see their prey (Kahl 1964, Kushlan 1978). The Yellow-billed Stork (*M. ibis*), which also feeds tactilely, is considered "mostly nocturnal" in its foraging habits (Fasola and Canova 1993).

McNeil et al. (1993) suggested three hypotheses for why colonial waterbirds would forage nocturnally. First, nocturnal feeding provides supplemental food when daytime foraging is insufficient to meet energetic demands; second it provides the most preferential (or profitable) foraging opportunities; and third it reduces predation risk.

Here we quantify the prevalence of nocturnal activities of Wood Storks in two settings: inland (freshwater) impoundments and a coastal roost site. Storks used both locations in the late summer and early fall months, after the breeding season was completed. Activity pat-

terns of Wood Storks are assessed in relation to hypotheses proposed by McNeil et al. (1993).

Methods.—The Kathwood impoundments are located in Aiken County, South Carolina (Coulter et al. 1987). Three impoundments (11.3 ha) are stocked with bluegill sunfish (*Lepomis macrochirus*) and brown bullhead (*Ameiurus natalis*) and partially drained to an appropriate depth for stork foraging (15 to 30 cm) during the late summer months. Impoundment fish densities range from 10 to 30 fish/m² when water levels are lowered. The Priest Landing roost site is a 1.6 ha brackish water impoundment partially surrounded by trees on the northern tip of Skidaway Island, Chatham County, Georgia.

Stork presence at the Kathwood Ponds was determined by observations made every 15 min from 1200 h to 1200 h EST during 10 observation periods (Table 1). Total counts of Wood Storks and other wading birds present and numbers of each species actively foraging were recorded at each observation interval. At the Priest Landing roost, storks and other wading birds in the roost were counted every hour from 1200 h to 1200 h in 1994 (09 to 10 August, 29 to 30 August, 19 to 20 September) and 1997 (10 to 11 September, 16 to 17 September, 29 to 30 September, 14 to 15 October).

Observers monitored stork presence or activity from a blind on the edge of each study site. We used 10 × 40 binoculars and a 20–60× spotting scope during the day and a Star-Tron (MK-505) night-vision system at night.

Activity patterns of Wood Storks at the Kathwood impoundments were categorized for three light-related periods: diurnal 0800 to 1800 h EST, crepuscular 0500 to 0800 h and 1800 to 2100 h EST, and nocturnal 2100 to 0500 h EST. Stork presence and activity could not be compared statistically with regard to those periods because the number of storks present was not independent across those periods.

TABLE 2. Results of quadratic regression analyses of the relationships between centered number of storks at roosting and foraging sites, time-of-day, and tide levels.

Source	Coefficient	SE	T	P	R ²
Kathwood Foraging Site/Number of Storks Present					
Constant	-47.66385	2.55681	19.25	<0.0001	0.42
Time	0.11962	0.00486	25.31	<0.0001	
Time × Time	-0.00005	0.00001	26.29	<0.0001	
Kathwood Foraging Site/Number of Storks Foraging					
Constant	-21.37560	2.45211	-8.72	<0.0001	0.12
Time	0.05061	0.00472	10.86	<0.0001	
Time × Time	-0.00002	<0.00001	-10.82	<0.0001	
Priest Landing Roost Site/Number of Storks Present					
Constant	-59.62513	6.11273	-9.75	<0.0001	0.55
Time	0.09797	0.00936	10.47	<0.0001	
Time × Time	-0.00004	<0.00001	-10.47	<0.0001	
Tide	-0.53564	1.24537	-0.43	0.668	
Tide × Time	0.00336	0.00090	3.75	<0.0001	

We used quadratic models to investigate relationships between time-of-day and Wood Stork abundance at both observation sites. Because the mean number of storks at foraging and roost sites varied greatly among observation periods, we centered observations by subtracting the mean number of Wood Storks for an observation period from each observation in that period. For the Kathwood foraging site, we used a simple quadratic equation, with time as the independent variable and centered number of storks present and number of storks foraging as dependent variables. For analytical purposes, time was coded so that 0:00 h was 12:00 noon on the day an observation began and 24:00 h was 12:00 noon on the day the observation was completed. With that coding system, 12:00 midnight fell at the center of the observation period, and if Wood Stork foraging were greater at night, then a unimodal pattern would be expected across the coded time scale.

To assess the potential role of tide at the Priest Landing roost site, we added tide and its interaction with time to the quadratic model as follows:

$$y = \alpha + \beta_1(x_1) + \beta_2(x_1^2) + \beta_3(x_2) + \beta_4(x_1x_2).$$

In the expanded model, y is the number of storks at the roost, x_1 is time, and x_2 is tide level. The parameters β_3 and β_4 related to effects of tide; significance of β_3 indicates change in the y -intercept of the curve as a function of tide, and significance of β_4 indicates a change in shape of the curve as a function of tide. Hourly tide level data were obtained from the NOAA Romerly Creek Station ~1 km from the roost site. For analytical purposes, time was coded so that observation periods ran from 12:00 midnight (0:00 h) to 12:00 midnight (24:00 h) by placing observations from the second 12 h portion of the observation period in front of observations from the first 12 h portion of the observation period. That coding placed the time period of expected highest roost attendance

(and assumed lowest foraging activity) in the middle of the observation period. For both models, we used least-squares methods to estimate parameter values (α and β) and t -tests to test the null hypothesis of parameter estimates equal to zero for all parameters in the models.

Results.—Although Wood Storks were present and foraged during all observation periods at Kathwood, twice as many storks were present during crepuscular and nocturnal periods than during the diurnal periods (Tables 1 and 2, Fig. 1A). Nocturnal foraging also was observed during all 10 periods, but was very limited (averaged <5 storks) during two periods. Analyses of numbers of foraging storks relative to time of day also demonstrated a significant unimodal pattern with more storks foraging at night than other times, although that was a considerably weaker relationship than that for stork presence (Table 2, Fig. 1B).

Wood Storks consistently used the Priest Landing roost in both years of study, with the average number of storks present per hour for the 24 h periods ranging from approximately 30 to 60. Stork attendance was significantly linked to time of day and its interaction with tide, but not specifically to tide (Table 2, Fig. 2). More storks were present in the roost during daylight hours than nocturnal hours (Fig. 3A). During low tide levels (<1.0 m), storks were away from the roost more during the nocturnal hours than daylight hours ($R^2 = 0.42$, $P < 0.00001$; Fig. 3B). During very high tide levels (>2.0 m), storks remained in the roost more at night ($R^2 = 0.41$, $P < 0.0001$; Fig. 3C), although data for the early morning hours (midnight to sunrise) were scarce.

Discussion.—Wood Storks using the Kathwood impoundments were present in larger numbers and foraged as much at night as during other times of day, although the relationship between the number of storks foraging and time-of-day was very weak. Wood Storks appeared to be foraging in 1 to 4 h

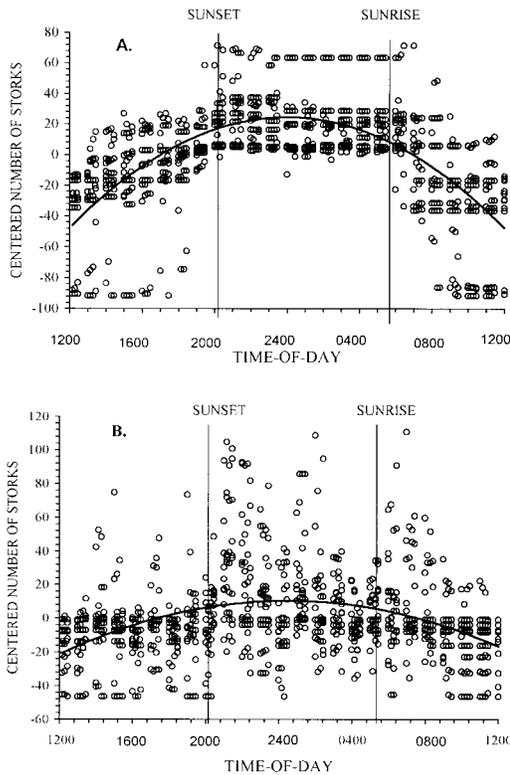


FIG. 1. Fit of a quadratic equation to describe Wood Stork use of the Kathwood impoundments (inland freshwater) relative to time of day: A. Total storks present. B. Number of foraging storks. Because the mean number of storks varied greatly among observation periods, we centered observations by subtracting the mean number of Wood Storks for an observation period from each observation in that period.

bouts interspersed with periods of little or no foraging activity (Fig. 4). Reasons for that periodicity in foraging are not known, although the pulse of foraging activity near sunrise could be linked to the arrival of other wading birds possibly stimulating the storks into activity. Stork attendance at the coastal Priest Landing roost was linked to time of day more so than to tide level, with higher attendance occurring during the day. Storks presumably departed that site to forage in tidal wetlands and tended to leave more when lower tides occurred during the nocturnal period than the diurnal period.

Of the three hypotheses proposed by McNeil et al. (1993) to explain nocturnal foraging in wading birds, predator avoidance is the least likely to contribute to stork nocturnality as free-ranging wading birds the size of storks have few documented predators (Kushlan 1978). Although storks undergo interregional movements (Kushlan 1981), the need for *supplemental*

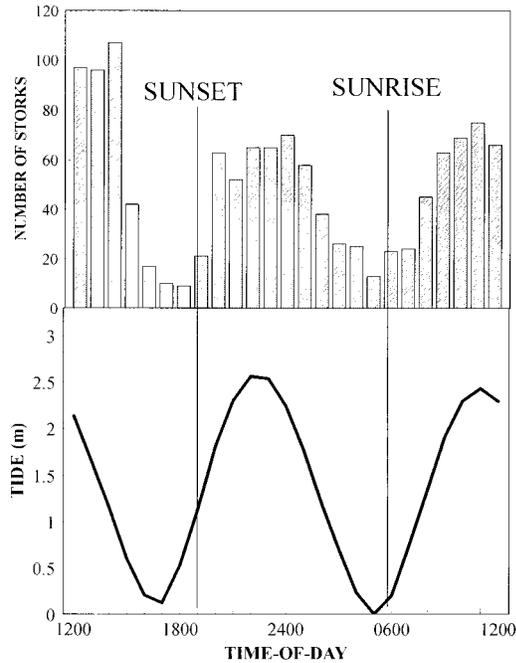


FIG. 2. Wood Stork attendance at the Priest Landing roost site in relation to tide level and time of day on 8 August 1994.

feeding is not thought to be the case here due to their relatively leisurely rate (several days including foraging stops) of travel to overwintering areas (Comer et al. 1987) and the fact that storks soar in thermals while doing so (Bryan et al. 1995). Moreover, the nocturnality observed in this study (August–October) occurred in a season when storks were not preparing for imminent long-distance travel.

Potential reasons for greater foraging success (preferential foraging) during the nocturnal periods are many. Wood Storks feed tactily more so than visually (Kushlan 1979) and should be as successful foraging during the nocturnal period as during daylight hours. Prey within the water column may have more difficulty seeing predatory storks in reduced light conditions. Also, freshwater prey species such as bullheads and catfish are more active nocturnally than diurnally (Darnell and Meierotto 1965) and thus should be more available as prey. Bluegill sunfish move into shallower waters after sunset in response to availability of their prey (Bauman and Kitchell 1974) and changes in dissolved oxygen concentrations, and may be more available as prey during these time periods.

Along the Georgia coast, tidal amplitude can be as great as 3.0 m. All surface water and potential prey in many marsh systems literally drain through one to multiple tidal creeks as water levels drop. Although Wood Storks typically do not forage in flowing fresh-

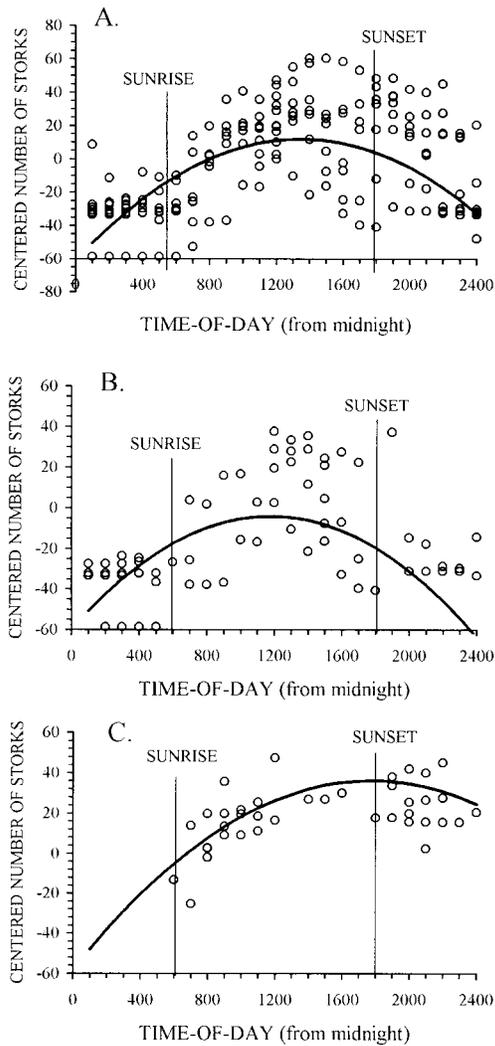


FIG. 3. Fit of a quadratic equation to describe Wood Stork attendance at the Priest Landing Roost relative to time of day: A. All observations ($n = 176$). B. Low tide observations (<1.0 m; $n = 68$). C. High tide observations (>2.0 m; $n = 39$). Because the mean number of storks varied greatly among observation periods, we centered observations by subtracting the mean number of Wood Storks for an observation period from each observation in that period.

water systems (Coulter and Bryan 1993), tidal creeks containing greatly concentrated prey should provide narrow bands of excellent foraging habitat for tactile predators approximately twice every 24 h. Also, prey species in estuarine systems, such as shrimp, are more active nocturnally (Shenker and Dean 1979).

Nocturnal foraging also may be important to storks due to reduced competition with diurnal wading bird

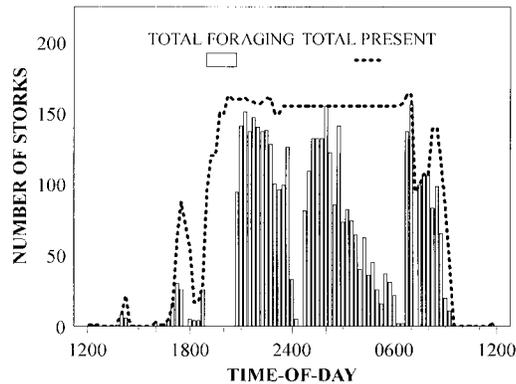


FIG. 4. Number of Wood Storks at the Kathwood impoundments on 17 to 18 July 1994. Foraging bouts (1 to 4 h long) were observed in all ten 24 h observation periods.

species. Great Egrets (*Ardea albus*) are the second most common wading bird using the Kathwood impoundments (after Wood Storks) and fed exclusively between sunrise and sunset on the impoundments. However, the interactions and competition between those two species require additional study. In the coastal roost, night herons (*Nycticorax* spp.) and Great Blue Herons (*Ardea herodias*) departure times typically approximated those of storks whereas Great Egrets and White Ibises (*Eudocimus albus*) tended to depart and return to the roost in the daylight hours.

Both sites were monitored for Wood Stork activity during the nonbreeding season and many of the study birds were prebreeding age (<3 years of age). Therefore those birds were fulfilling only their own energetic needs and were not constrained by attendance or energetic requirements associated with rearing young. The decision to forage actively was linked to the period when foraging conditions were probably optimal in regards to prey abundance, "catchability," and reduced competition. Maximizing foraging efficiency increases survival and the ability to reproduce successfully (Krebs 1978). Increased foraging efficiency through nocturnal foraging enhances the ability of adult storks to recover from the rigors of the breeding season and aides younger birds in their attempts to develop foraging skills for survival and eventually reach breeding age.

An appreciation of the high degree of nocturnality of those storks during the postbreeding season can help to insure efforts to define and protect critical foraging habitats used by storks. A reassessment of the degree to which certain proposed nighttime human disturbances or activities (e.g. dredging, fishing, and shrimping) might negatively affect the foraging of Wood Storks in the area is needed, as well as the methods by which wetland systems are monitored for stork use.

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LITERATURE CITED

- BAUMAN, P. C., AND J. F. KITCHELL. 1974. Diel patterns of distribution and feeding of bluegill (*Lepomis macrochirus*) in Lake Wingra, Wisconsin. *Transactions of the American Fisheries Society* 103:255–260.
- BENT, A. C. 1926. Life histories of North America marsh birds. Smithsonian Institution, U.S. National Museum Bulletin 135.
- BRYAN, A. L., JR., M. C. COULTER, AND J. C. PENNYCUICK. 1995. Foraging strategies and energetic costs of foraging flights by breeding Wood Storks. *Condor* 97:133–140.
- COMER, J. A., M. C. COULTER, AND A. L. BRYAN, JR. 1987. Overwintering locations of Wood Storks captured in east-central Georgia. *Colonial Waterbirds* 10:162–165.
- COULTER, M. C., AND A. L. BRYAN, JR. 1993. Foraging ecology of Wood Storks (*Mycteria americana*) in east-central Georgia. I. Characteristics of foraging sites. *Colonial Waterbirds* 16:59–70.
- COULTER, M. C., W. D. MCCORT, AND A. L. BRYAN, JR. 1987. Creation of artificial foraging habitat for Wood Storks. *Colonial Waterbirds* 10:203–210.
- DARNELL, R. M., AND R. R. MEIEROTTO. 1965. Diurnal periodicity in the black bullhead, *Ictalurus melas* (Rafinesque). *Transactions of the American Fisheries Society* 94:1–9.
- FASOLA, M., AND L. CANOVA. 1993. Diel activity of resident and immigrant waterbirds at Lake Turkana, Kenya. *Ibis* 135:442–450.
- KAHL, M. P. 1964. Food ecology of the Wood Stork (*Mycteria americana*) in Florida. *Ecological Monographs* 34:97–117.
- KREBS, J. R. 1978. Optimal foraging: Decision rules for predators. Pages 23–63 in *Behavioral Ecology, an Evolutionary Approach* (J. R. Krebs, and N. B. Davies, Eds.). Blackwell Scientific Publications, London.
- KUSHLAN, J. A. 1978. Feeding ecology of wading birds. Pages 249–297 in *Wading Birds* (A. Sprunt IV, J. C. Ogden, and S. Winkler, Eds.). National Audubon Society Research Report 7. New York.
- KUSHLAN, J. A. 1979. Prey choice by tactile-foraging wading birds. *Proceedings of the Colonial Waterbird Group* 3:133–142.
- KUSHLAN, J. A. 1981. Resource use strategies of wading birds. *Wilson Bulletin* 93:145–163.
- MCNEIL, R., P. DRAPEAU, AND R. PIEROTTI. 1993. Nocturnality in colonial waterbirds: Occurrence, special adaptations, and suspected benefits. *Current Ornithology* 10:187–245.
- SHENKER, J. M., AND J. M. DEAN. 1979. The utilization of an intertidal salt marsh creek by larval and juvenile fishes: Abundance, diversity and temporal variation. *Estuaries* 2:154–163.

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Timing of Breeding Range Occupancy Among High-latitude Passerine Migrants

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ABSTRACT.—The brief subarctic summer limits the time available for birds to complete their reproductive activities, yet the temporal requirements of high-latitude passerine migrants are not well understood. Our analyses examined the timing of spring and au-

turn migration among 18 passerine species to obtain indirect estimates of the time they occupy their breeding ranges in northwestern North America. From 1992 to 1998, the Alaska Bird Observatory (64°50'N, 147°50'W) banded 31,698 individuals during the most intensive standardized mist-netting study ever conducted in subarctic North America. Among the migrants examined, the estimated num-

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ber of days that species were present in interior Alaska ranged from 48 days for adult Alder Flycatchers (*Empidonax alnorum*) to 129 days for American Robins (*Turdus migratorius*). Adults departed significantly later in autumn than immatures in 10 of 18 species we examined and significantly earlier than immatures in only one species, Alder Flycatcher. Breeding range occupancy of Nearctic–Neotropical migrants occurs in this region within the range of average frost-free temperatures in Fairbanks, Alaska, and is significantly shorter in duration than among Nearctic–Nearctic (“short-distance”) migrants at this latitude.

The high latitudes of North America support a diverse avifauna, because during the summer months the region is characterized by a nutrient-rich environment, an extended photoperiod, and a hospitable climate. But summer at high latitudes is brief. For example, the average frost-free period in Fairbanks, Alaska was 105 days from 1905 to 1999 (from 20 May to 2 September; National Weather Service data). Birds that migrate to Alaska are therefore under greater temporal pressure to complete breeding-season activities (such as territory and mate acquisition, nest building, egg laying, incubation, care of young, and molt) than birds at lower latitudes. Yet, the total amount of time passerines spend completing the breeding effort is not well known. Few studies have been conducted over the entire breeding season at high latitudes, and those studies that have examined breeding chronology at northern locations (e.g. Rimmer 1988) may not accurately document departure from the breeding grounds because of small samples and postbreeding dispersal.

Studies sampling migrant passage during spring and autumn provide an indirect measure of time spent on the breeding grounds. The accuracy of that measure increases with proximity to a population’s breeding area. We sampled migrants near the northern and western limits of their migrations during spring and autumn. Here we examine timing of passage at the species level in that region to obtain indirect estimates of the time birds occupy their breeding ranges in the northwestern extreme of North America. Additionally, we answer the following questions: (1) How compressed are breeding-season activities among high-latitude migrants? (2) Do Nearctic–Neotropical migrants differ from Nearctic–Nearctic (“short-distance”) migrants in the timing of breeding-range occupancy?

Study area and methods.—The study area is located in Fairbanks, Alaska (64°5′N, 147°5′W), near the confluence of the Chena and Tanana rivers (elevation 130 m). The Tanana Valley is a well documented migration corridor for many species of birds, including Sandhill Cranes (*Grus canadensis*; Kessel 1984), many species of raptors (McIntyre and Ambrose 1999), waterfowl, shorebirds, and passerines (Cooper and Ritchie 1995).

TABLE 1. Net-hours of operation and total days of netting in spring and autumn at Creamer’s Field Migration Station in Fairbanks, Alaska (1992–1998).

Year	Spring		Fall	
	Net-hours	Days	Net-hours	Days
1992	6,903	42	5,822	46
1993	10,552	43	13,472	50
1994	11,252	41	13,935	52
1995	12,731	45	13,944	57
1996	12,411	44	14,985	57
1997	7,548	42	14,617	66
1998	6,800	39	11,853	54
Total	68,196	296	88,627	382

The study site, at Creamer’s Field Migration Station (CFMS), encompasses ~20 ha of the southwestern portion Creamer’s Field Migratory Waterfowl Refuge (731 ha). It is owned by the State of Alaska and operated by the Alaska Department of Fish and Game. The northern portion of CFMS is dominated by mature willow (*Salix* spp.) and paper birch (*Betula papyrifera*) bordering a seasonally flooded wetland dominated by sedges (*Carex* spp.) and one grass species (*Calamagrostis canadensis*). The central section of the study area is characterized by late successional white spruce (*Picea glauca*) and balsam poplar (*Populus balsamifera*). The southern portion of the study area has trembling aspen (*Populus tremuloides*), balsam poplar, and willow growing near an agricultural field. Except for the agricultural field, that mosaic of habitat types is representative of the habitats occurring in the boreal forest floodplains of interior Alaska.

A standardized mist-netting protocol was conducted at CFMS from 1992–1998 using an array of 22–50 standard mist nets (30 mm mesh, 2.6 × 12 m). Nets were arranged in a north–south direction, perpendicular to the Tanana Valley migration corridor, and operated daily from 0600 to 1300 (Alaska) during spring migration (25 April–15 June). During autumn migration (15 July–30 September), nets were opened at approximately sunrise and closed 7 h later. Sampling at the ends of both seasons (10–15 June and 25–30 September) was limited to every other day. Nets were closed during inclement weather. Fewer nets were operated in 1992, 1997, and 1998 than in other years (Table 1), and nets were not operated between 17 July and 2 August 1992.

Birds were banded with U.S. Fish and Wildlife Service bands, and data were collected to determine age (autumn only, using degree of skull ossification), and breeding condition (spring only, using incubation patches in females and enlarged cloacal protuberances in males). During autumn migration, estimates of the percentage of juvenal plumage were recorded for first-year individuals.

To ensure independence of records in those analyses, we used only initial captures of individuals (all subsequent captures of individuals were eliminated). We also excluded local breeders on the basis of the following criteria: females with incubation patches, individuals captured more than seven days from first capture, and birds captured in one season and recaptured in another. First captures of individuals were also removed if they were later recaptured with breeding characteristics. Finally, we excluded first-year birds with >30% of their body in juvenal plumage, because we considered them nonmigratory at that time.

We defined Nearctic–Neotropical migrants as those species with all or part of their populations breeding north of the Tropic of Cancer and all or part of the same populations wintering south of that line (Rappole et al. 1983). We defined Nearctic–Nearctic migrants as those species whose breeding and wintering populations are primarily north of the Tropic of Cancer. Those species are often categorized as short-distance migrants.

A maximum estimate of time spent on breeding grounds was obtained from the difference between median dates of spring and autumn passage. We did not standardize numbers of birds captured by unit of netting effort for two reasons. First, net hours (nh) were uniformly distributed among days when all years were combined during spring (Kolmogorov–Smirnov-test, $D_{max} = 0.08$, $n = 68,196$, $P > 0.10$) and autumn (KS-test, $D_{max} = 0.07$, $n = 87,627$, $P > 0.10$). Second, standardizing captures by unit of netting effort can impart bias by artificially inflating or deflating sample sizes. For example, 18 birds captured during 80 nh could provide sample sizes of 22.5 birds/100 nh, 225 birds/1,000 nh, or .225/nh. Thus, an arbitrary number of net-hours used to standardize captures directly affects sample size, which affects the power in statistical tests. Finally, manipulating sample size in our study was not necessary given the uniformity of net-hours within seasons.

Differences in timing of passage were present among years for some species (Benson 2000). Here we combined all years to increase sample sizes because that provides the best species-level estimate of the duration of breeding-range occupancy. Additionally, variation in the netting effort in earlier years was minimized when years were pooled because nets were operated uniformly among days within each season when all years were combined.

We tested for differential timing of migration between adults and immatures during autumn using the Mann–Whitney U test. Differences in timing of migration between age classes could affect species-level estimates of the median date of autumn passage, because most autumn captures at that study site are first-year birds.

Results.—During 1992–1998, staff of the Alaska Bird Observatory accumulated 68,196 nh during spring and 88,627 nh during autumn (Table 1). Dur-

ing those seven years, 31,698 birds of 58 species were banded. We examined the timing of passage of 25,718 individuals among 18 passerine species. Judging from capture distributions (Benson 2000), the netting periods spanned the entire spring and autumn migration periods for all species analyzed except Alder Flycatcher. Spring netting was truncated shortly after peak passage of that species. Therefore, for that species median spring passage dates may be slightly later than presented here.

There were significant differences in median dates of autumn passage between adults and immatures in 11 of 18 species (Table 2). The Alder Flycatcher was the only species in which the departure date of adults preceded that of immatures; that difference averaged 13 days (Table 2). In Ruby-crowned Kinglets, Swainson's Thrushes, American Robins, Orange-crowned Warblers, Yellow-rumped Warblers, Yellow Warblers, Blackpoll Warblers, Wilson's Warblers, American Tree Sparrows, White-crowned Sparrows, and Dark-eyed Juncos, immatures preceded adults (Table 2). The largest significant age-related differences in passage dates occurred among Wilson's Warblers and Dark-eyed Juncos; in both species, adults migrated on average 13 days later than immatures. In 6 of 18 species, there were no significant differences between adults and immatures in median dates of passage. Because there were significant age-related differences in departure dates in several species, and because inference of departure is conflated by large numbers of immatures (lowering accuracy; Table 2), immatures were eliminated from all subsequent analyses.

Estimates of the period that adults occupied their breeding ranges were more condensed for Nearctic–Neotropical migrants ($n = 12$) than for Nearctic–Nearctic migrants ($n = 6$; Mann–Whitney $U = 71.0$, $P < 0.05$; Table 2, Fig. 1). The mean period of breeding-range occupancy for all Nearctic–Neotropical migrants was 90.6 days (SE = 4.4 days), or <25% of the annual cycle. Nearctic–Nearctic migrants averaged 119.8 days (SE = 3.4 days), or 33% of the annual cycle.

The estimated number of days that adults were present in interior Alaska ranged from 48 days for Alder Flycatchers to 129 days for American Robins (Fig. 1). The next-briefest times occurring between median dates of spring and autumn passage in Yellow Warblers, Hammond's Flycatchers, and Northern Waterthrushes, which spent 84, 86, and 86 days, respectively, on their breeding ranges, or ~23% of the annual cycle.

Discussion.—The later departure dates of adults in many species may be explained by the timing of molt in adults, which, unlike immatures, replace flight feathers in autumn. Differences in timing of passage between adult and immature Swainson's Thrushes, although present here, were not at Long Point, Ontario, western Pennsylvania, or coastal Alabama in

TABLE 2. Timing of migration during spring and autumn, and differences in passage dates between adults and immatures during autumn among passerine species in Fairbanks, Alaska (1992–1998).

Species	Status ^a	Spring migration				Autumn migration				Z ^c	Days ^d	
		Adults		Immatures		Adults		Immatures				
		n	Range	Date ^b	n	Range	Date ^b	n	Range			Date ^b
Alder Flycatcher (<i>Empidonax alnorum</i>)	L	39	154–167	161	83	196–237	209	342	204–256	222	8.81**	48
Hammond's Flycatcher (<i>Empidonax hammondi</i>)	L	58	115–166	138	19	198–259	224	226	196–249	216	1.66	86
Ruby-crowned Kinglet (<i>Regulus calendula</i>)	S	46	116–143	130	107	226–269	253	846	198–273	245	4.32**	123
Gray-cheeked Thrush (<i>Catharus minimus</i>)	L	102	135–159	144	45	199–265	242	187	211–261	239	2.76*	98
Swainson's Thrush (<i>Catharus ustulatus</i>)	L	283	132–159	145	82	224–270	240	675	198–268	232	7.24**	95
American Robin (<i>Turdus migratorius</i>)	S	217	121–167	137	77	235–271	266	198	205–272	249	6.66**	129
Orange-crowned Warbler (<i>Vermivora celata</i>)	L	252	130–164	143	582	196–266	245	3,378	196–270	237	8.63**	102
Yellow-rumped Warbler (<i>Dendroica coronata</i>)	L	539	117–163	136	376	208–268	244	5,663	196–266	234	5.49**	108
Yellow Warbler (<i>Dendroica petechia</i>)	L	149	135–167	151	94	199–264	235	734	196–260	227	7.42**	84
Blackpoll Warbler (<i>Dendroica striata</i>)	L	69	135–160	142	37	223–266	236	359	209–256	231	4.07**	94
Northern Waterthrush (<i>Seiurus noveboracensis</i>)	L	210	133–159	143	12	221–237	229	221	197–252	227	1.15	86
Wilson's Warbler (<i>Wilsonia pusilla</i>)	L	242	129–162	144	90	207–271	242	822	198–271	229	9.58**	98
American Tree Sparrow (<i>Spizella arborea</i>)	S	88	117–153	131	501	236–271	257	3,224	224–274	256	3.53**	126
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	L	197	126–167	143	30	198–268	235	536	197–270	231	2.55*	92
Fox Sparrow (<i>Passerella iliaca</i>)	S	48	115–147	131	64	228–264	247	221	199–269	244	2.44*	116
Lincoln's Sparrow (<i>Melospiza lincolni</i>)	L	71	124–167	139	60	196–269	235	1,259	196–273	229	1.28	96
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	S	93	123–156	135	37	198–266	240	416	204–271	230	4.98**	105
Dark-eyed Junco (<i>Junco hyemalis</i>)	S	213	116–166	135	231	221–272	256	2,710	197–272	246	4.12**	121

^a L = Nearctic–Neotropical migrant, S = Nearctic–Nearctic migrant.

^b Median Julian dates of passage.

^c Results from Mann-Whitney U tests for differences in passage dates between adults and immatures in autumn.

^d Maximum estimate of the average number of days adults occupy breeding range (difference between median dates of spring and autumn passage).

* $P < 0.05$, ** $P < 0.003$ (significance with Bonferroni corrections).

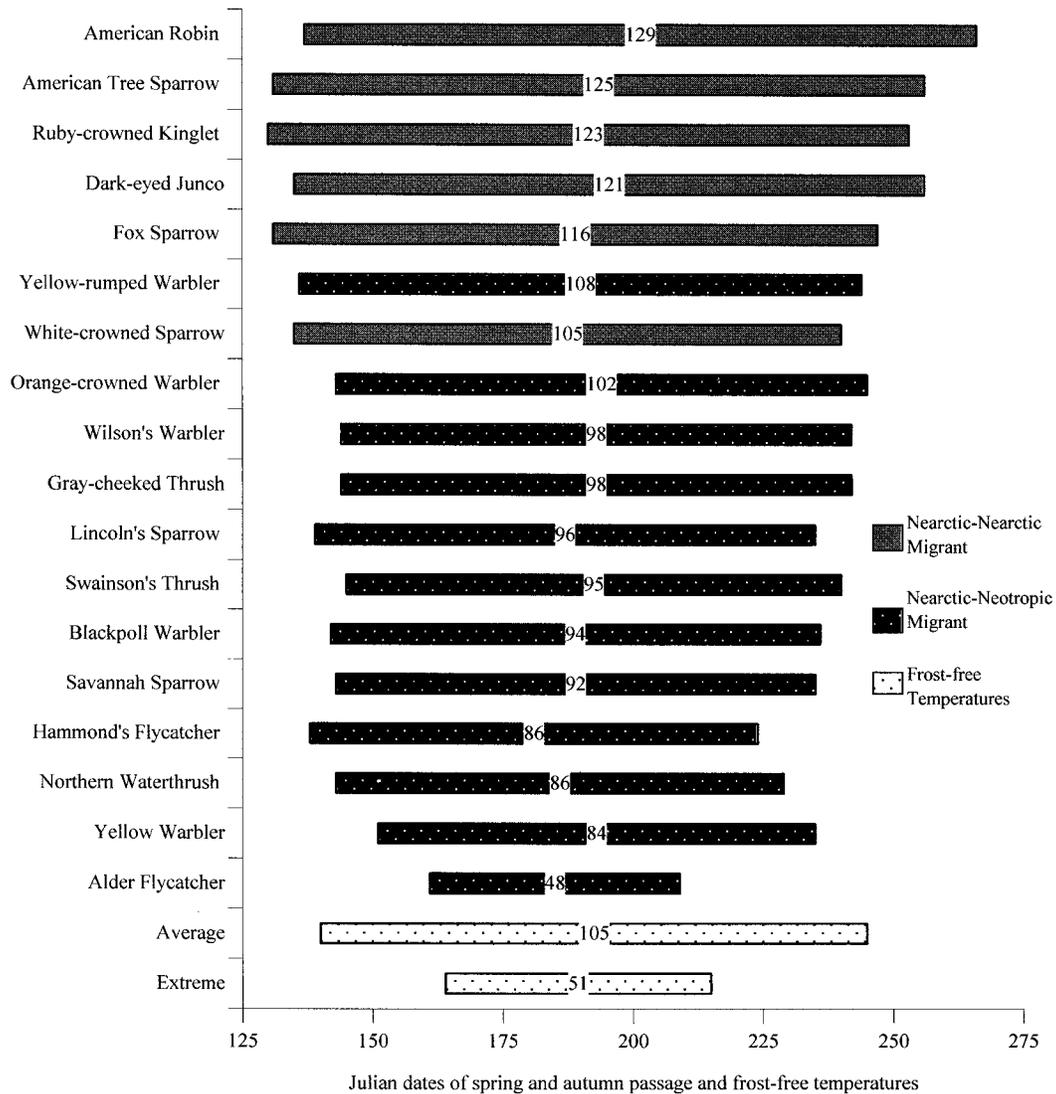


FIG. 1. Species-level estimate of the number of days passerine migrants occupy breeding ranges in Alaska using median dates of spring and autumn passage. Number of frost-free days are calculated from temperature records ($n = 95$ years) in Fairbanks, Alaska.

1990 (Woodrey and Chandler 1997). The same was true for 1991, with the exception of Long Point, where the median date of passage of adults was significantly earlier than immatures (Woodrey and Chandler 1997).

The Alder Flycatcher was the only species in our study in which adults preceded immatures in autumn. We estimated that adult Alder Flycatchers departed 13 days earlier than immatures, which is similar to previous results from Long Point, Ontario where a 14 day difference was found (Hussel 1991a). The lack of molt

in adults of that species prior to autumn migration (Dwight 1900) probably accounts for this difference.

Studies at lower latitudes have suggested that the duration of the breeding season for some Nearctic-Neotropical migrants is brief. Winker et al. (1992) studied passerine migration in Minnesota at $\sim 45^\circ\text{N}$ and concluded that many species spend $<30\%$ of their annual cycle on their breeding grounds. In this study, at $64^\circ 5'\text{N}$ and much nearer to the final destinations of high-latitude migrants, we estimated that populations of Nearctic-Neotropical migrants cap-

tured at our study site occupy their breeding ranges for <25% of their annual cycles, and that Nearctic–Nearctic migrants average 33% of their annual cycles on those high-latitude breeding ranges.

The 48 day difference between median spring and autumn passage dates of Alder Flycatchers in interior Alaska suggests that that species spends just 13% of its annual cycle on those northern breeding grounds. That is the shortest period of breeding range occupancy yet documented for a population or species of migratory passerine. In comparison, a lower-latitude study estimated 73 days between median dates of spring and autumn passage of Alder Flycatchers (adults only; Hussel 1991a, b).

We estimated that some Alaska populations of Yellow Warblers occupied their breeding range for 84 days, which suggests decided compression when compared with the 104 days estimated to be required to accomplish breeding-season activities in Manitoba, at 50°1'N (Busby and Sealy 1979). Other studies of Yellow Warblers also indicate that breeding activities at high latitudes are indeed compressed. Studies by Briskie (1995) and Rimmer (1988) provide an estimate of 79–115 days required by Yellow Warblers for breeding range activities at other high-latitude sites, and that is concordant with our estimate of 84 days for completion of breeding season activities for this species in interior Alaska.

Breeding-season activities begin later in Alaska compared with other latitudes. For example, in Palomar County, California, juvenile Swainson's Thrushes have been observed as early as 15 May (Johnson and Geupel 1996), and juvenile Wilson's Warblers have been observed as early as 15 April (Chase et al. 1997). The median date of spring arrival of adults of those two species in Fairbanks, Alaska, does not occur until 15 May. Further, in Orange-crowned Warblers, nest construction has been observed in early March on Channel Island, California (Sogge et al. 1994). In contrast, Orange-crowned Warblers do not arrive in central Alaska until ~75 days later.

The latest date on which freezing temperatures have occurred in spring in Fairbanks was 13 June (1922), and the earliest date of freezing temperatures in autumn was 3 August (1944; based on a 95-year National Weather Service record). At the extreme, therefore, that region has the possibility of delivering only 51 consecutive days of temperatures greater than 0°C. In that region, Alder Flycatchers arrive near the record last date of frost in spring and leave before the record first date of frost in autumn (Fig. 1). That is probably not a coincidence. It is well known that flying insect availability is negatively affected by frosts, and that would seem to provide strong selection against Alder Flycatchers' occupation of their breeding grounds during times of potential frost. Other insectivorous birds probably forage on a more diverse prey base when flying insects

are not available and are therefore able to withstand early and late frosts in extreme years.

Summer at high latitudes is brief. Nearctic–Nearctic migrants averaged 119.8 days between spring and autumn median dates of passage, and Nearctic–Neotropical migrants averaged 90.6 days. All but one Nearctic–Neotropical species, the Yellow-rumped Warbler, appeared to time their arrivals and departures to occur within the long-term average of 105 days of frost-free temperatures in Fairbanks, Alaska (Fig. 1). Nearctic–Neotropical migrants rely primarily on insects for food, and are likely to be present as that resource waxes, becomes abundant, and then wanes. Conversely, most of the Nearctic–Nearctic species we studied rely on a seed- or fruit-dominant diet in winter, accounting for their ability to be present during periods of frost and indeed frozen conditions. Further, Nearctic–Nearctic migrants may be better adapted to adverse climatic conditions, which they may also experience on wintering areas. In northwestern North America, the Nearctic–Neotropical migrants we studied time their breeding-range occupancy to occur within the summer frost-free period and complete their annual reproductive cycle in a brief temporal window.

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LITERATURE CITED

- BENSON, A. M. 2000. Temporal patterns of migration, molt, and fat storage among high-latitude passerine migrants. M.S. thesis, University of Alaska Fairbanks, Fairbanks.
- BRISKIE, J. V. 1995. Nesting biology of the Yellow Warbler at the northern limit of its range. *Journal of Field Ornithology* 66:531–543.
- BUSBY, D. G., AND S. G. SEALY. 1979. Feeding ecology of a population of nesting Yellow Warblers. *Canadian Journal of Zoology* 57:1670–1681.

- CHASE, M. K., N. NUR, AND G. R. GEUPEL. 1997. Survival, productivity, and abundance in a Wilson's Warbler population. *Auk* 114:354–366.
- COOPER, B. A., AND R. J. RITCHIE. 1995. The altitude of bird migration in east-central Alaska: A radar and visual study. *Journal of Field Ornithology* 66:590–608.
- DWIGHT, J., JR. 1900. The sequence of plumages and moults of passerine birds of New York. *Annals of the New York Academy of Sciences* 13:73–360.
- HUSSEL, D. J. T. 1991a. Fall migrations of Alder and Willow flycatchers in southern Ontario. *Journal of Field Ornithology* 62:260–270.
- HUSSEL, D. J. T. 1991b. Spring migrations of Alder and Willow flycatchers in southern Ontario. *Journal of Field Ornithology* 62:69–77.
- JOHNSON, M. D., AND G. R. GEUPEL. 1996. The importance of productivity to the dynamics of a Swainson's Thrush population. *Condor* 98:133–141.
- KESSEL, B. 1984. Migration of Sandhill Cranes, *Grus canadensis*, in east-central Alaska, with routes through Alaska and western Canada. *Canadian Field-Naturalist* 98:279–282.
- MCINTYRE, C. L., AND R. E. AMBROSE. 1999. Raptor migration in autumn through the Upper Tanana River Valley, Alaska. *Western Birds* 30:33–38.
- RAPPOLE, J. H., E. S. MORTON, T. E. LOVEJOY III, AND J. L. RUOS. 1983. Nearctic Avian Migrants in the Neotropics. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C.
- RIMMER, C. C. 1988. Timing of the definitive prebasic molt in Yellow Warblers at James Bay, Ontario. *Condor* 90:141–156.
- SOGGE, M. K., W. M. GILBERT, AND C. VAN RIPER III. 1994. Orange-crowned Warbler (*Vermivora celata*). In *The Birds of North America*, no. 101 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- WINKER, K., D. W. WARNER, AND A. R. WEISBROD. 1992. Migration of woodland birds at fragmented inland stopover site. *Wilson Bulletin* 104:580–598.
- WOODREY, M. S., AND C. RAY CHANDLER. 1997. Age-related timing of migration: Geographic and interspecific patterns. *Wilson Bulletin* 109:52–67.

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Growth Rate and Energetics of Arabian Babbler (*Turdoides squamiceps*) Nestlings

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ABSTRACT.—Arabian Babblers (*Turdoides squamiceps*) are territorial, cooperative breeding passerines that inhabit extreme deserts and live in groups all year round. All members of the group feed nestlings in a single nest, and all group members provision at similar rates. Nestlings are altricial and fledge at about 12 to 14 days, which is short for a passerine of its body mass. Because parents and helpers feed nestlings, we hypothesized that the growth rate of nestlings is fast and that they fledge at a body mass similar to other passerine fledglings. Using a logistic growth curve, the growth rate constant (k) of nest-

lings was 0.450, which was 18% higher than that predicted for a passerine of its body mass. Asymptotic body mass of fledglings was 46 g, which was only 63% of adult body mass, a low percentage compared to other passerines. Energy intake retained as energy accumulated in tissue decreased with age in babbler nestlings and amounted to 0.29 of the total metabolizable energy intake over the nestling period. However, energy content per gram of body mass increased with age and averaged 4.48 kJ/g body mass. We concluded that our hypothesis was partially confirmed. Growth rate of babbler nestlings was relatively fast compared to other passerine species, but fledgling mass was relatively low.

Deserts are characterized by unpredictable rainfall and unpredictable, often sparse, food availability

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(Evenari et al. 1982), which can lead to a relatively slow growth rate of nestlings. The Arabian Babbler (*Turdoides squamiceps*) inhabits extreme deserts, which suggests that the growth rate of babbler nestlings would be slow. However, that does not appear to be the case because nestlings fledge at 12 to 14 days (Zahavi 1990), which is short compared to passerines of similar body mass (Ricklefs 1968). Consequently, nestlings have either a fast growth rate or they fledge at a low body mass, or both.

Arabian Babblers are cooperative breeders and parents and helpers participate in the feeding of nestlings. All group members provision at similar rates, irrespective of sex or dominance rank within the group (Wright 1997, 1998) and, therefore, we hypothesized that the growth rate of nestlings is fast. To test that hypothesis, we determined growth rate of babbler nestlings using a logistic growth curve and compared results with other passerines. We also measured energy use in babbler nestlings and estimated body-energy accumulation during growth.

Materials and Methods.—Study species and study site.—The Arabian Babbler (65 to 85 g) is a passerine species distributed in Saudi Arabia, Sinai, and in some of the extreme deserts of Israel, and is the only bird species in Israel that lives in groups year round. Those groups are territorial with the number of birds per group generally between 3 and 5 individuals, but the range is between 2 and 22 (Zahavi 1990).

Egg laying in each group of babblers takes place in one nest usually between February and August. Three clutches are possible. Breeding females lay between 3 and 5 eggs during each clutch and, where more than one female lays, the total number of eggs can reach 13. Maximum number of fledglings from one nest is about six. All members of the group participate in all phases of nesting and rearing young (Zahavi 1989, 1990).

All birds, including nestlings, were color banded. To determine growth rate of nestlings, 77 chicks from 24 nests were used; all nests were attended by parents and helpers. Five nests had a brood of two, 10 had a brood of three, 8 had a brood of four, and 1 had a brood of five. All nests were observed daily, and time of hatching was determined in each. Age of nestlings was measured in days. Changes in body mass of nestlings were followed by periodically weighing them over the nesting period and pooling the total of 547 measurements that were made (Degen et al. 1992).

The study was done at the Nature Reserve at Hatzeva (30°45'N; 35°15'E) in the Arava, ~30 km south of the Dead Sea. That site is characterized by long, hot, dry summers. It has a winter rainfall that averages 35 mm annually, but there are large variations in total rainfall and in its temporal and spatial distribution. Average daily air temperature for the hottest (August) and coldest (January) months are 30°C and 15°C, respectively (Stern et al. 1986).

Doubly labelled water measurements.—Field metabolic rate (FMR) and water flux of babbler nestlings were measured from February to August, 1996. Nestlings ($n = 65$) were injected subcutaneously with 70 μ l/g water whose oxygen was 95% ^{18}O and whose tritium produced 1.85 MBq/mL. Injections were done between 0900 and 1100 (GMT + 2 h). One hour was allowed for equilibration of the isotopes with body fluids (Degen et al. 1981), after which time a blood sample was collected from a brachial vein and the nestling was weighed on an electronic balance (± 0.2 g). Further blood samples were taken daily for the next one to two days at the same hour.

Blood samples were microdistilled under vacuum until dryness to obtain pure water. Specific activity of tritium in the water was measured by liquid scintillation spectrometry (Nagy 1983). Level of ^{18}O specific activity was measured by an autogamma counting system (Packard) after converting ^{18}O to gamma-emitting ^{18}F by cyclotron-generated proton activation (Wood et al. 1975). Blood samples from three noninjected nestlings from different nests were treated similarly to measure background levels of ^{18}O and tritium.

Total body water (TBW) of each nestling was calculated from the initial dilution volume of isotopic water, and water fluxes were calculated from the subsequent decline in specific activity of tritium over time (Degen et al. 1981). We were suspect of the exact injection volume in some nestlings and, therefore, there were 48 TBW measurements of the 65 injected nestlings. In nestlings without TBW measurement, TBW values from the regression analysis of TBW on body mass was used (see results) to calculate water flux and FMR (Anava et al. 2001). Total body solids were calculated as the difference between body mass and total body water. Rates of CO_2 production were estimated from the declines in specific activities in tritium and ^{18}O over time (Nagy 1980). Eight samples could not be measured for ^{18}O and, therefore, there were 57 FMR measurements.

Treatment of data.—A logistic equation was used to describe the growth curve of nestlings (Ricklefs 1968). We calculated the age of maximum growth rate (in days) and maximum growth rate (in grams per day) at the inflection point. To compare the growth rate of Arabian Babbler nestlings with other bird species, we determined the time required to grow from 10 to 90% (t_{10-90}) of asymptotic body mass (Ricklefs 1968).

Rates of CO_2 production of babbler nestlings were converted to rates of heat production and energy intake on the basis of an insect diet: 25.7 J were expended per milliliter of CO_2 produced (Nagy 1983) and metabolizable energy was 0.75 of gross energy (Robbins 1983). We assumed water influx equalled metabolic and preformed water from food. For insects, a volume of 0.660 μ l of metabolic water was generated per milliliter of CO_2 produced (Nagy

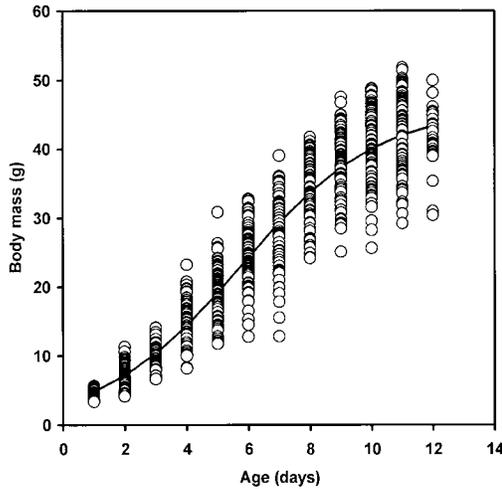


FIG. 1. Body mass of Arabian Babbler nestlings in relation to age. The line represents the logistic growth curve (see text).

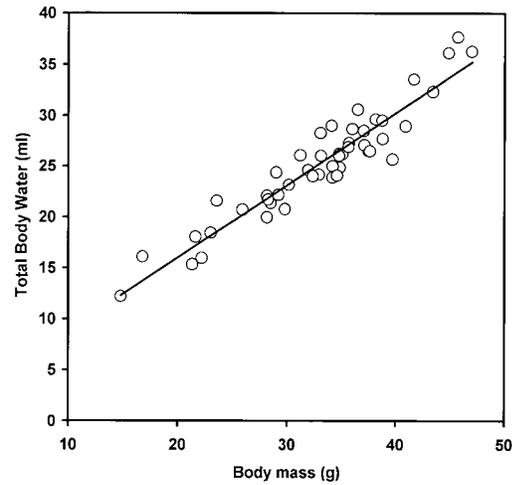


FIG. 2. Total body water volume of Arabian Babbler nestlings in relation to body mass.

1983). Preformed water intake was calculated as the difference between water influx and metabolic water.

We used FMR, growth rate, and changes in total body solids to calculate the energy budget of nestlings. Metabolizable energy intake (MEI) of the growing Arabian Babbler nestlings was expressed in terms of heat production (HP) plus or minus energy retention (ER) accumulated in new tissue. HP was estimated from the DLW measurements and ER from the changes in body solids of the growing nestlings, assuming that 21.3 kJ were accumulated as body energy per gram of body solid gain (Weathers and Sullivan 1991). Dry-matter intake was calculated from the MEI, assuming 20.3 kJ of metabolizable energy were yielded per gram dry matter (Nagy 1983). Fresh-matter intake was the sum of dry matter and preformed water of the diet. Total ER as a fraction of total MEI was determined on a daily basis and over the whole nestling period.

Results.—Nestling development and growth.—Arabian Babblers at hatching weighed 4.47 ± 0.61 g ($n = 37$) or 6.2% of adult body mass. Hatchlings were completely naked and their eyelids were fused. Their eyes opened between four and six days, during which time feathers emerged. As fledglings, aged 12 to 14 days, their bodies were covered with plumage, but development of wings and tail were not complete and, as a result, they were unable to fly. Tarsus length on day 10 (36.7 ± 1.53 mm, $n = 24$) was 96.6% of adult size (38.8 ± 0.91 mm, $n = 110$).

From the growth curve ($n = 547$) of nestlings ($n = 77$) described by the logistic curve (Fig. 1; Appendix), the asymptotic body mass of the babblers was 46.0 g and the constant parameters B and k were 13.3 and 0.450, respectively. The ratio between asymptote

body mass and mean adult mass (72 g) was 0.63. Maximum growth rate of nestlings, 5.17 g/day, was attained at 5.74 days and the time required to grow from 10 to 90% of asymptotic body mass (t_{10-90}) was 9.76 days

Total body water, water flux and field metabolic rate.—Total body water volume (TBW; in milliliters), estimated from ^{18}O space, increased linearly with body mass (m_b ; in grams), $\text{TBW} = 0.711 m_b + 1.781$ ($n = 48$; $S_b = 0.36$; $S_{y,x} = 1.75$; $r^2 = 0.89$; and $P < 0.001$, Fig. 2). However, TBW, as a fraction of body mass, decreased linearly with body mass (in grams), $\text{TBW} = 0.861 - 0.0028 m_b$ ($n = 48$; $S_b = 0.001$; $S_{y,x} = 0.06$; $r^2 = 0.11$; and $P < 0.05$).

Both water influx and water efflux increased linearly with body mass. The regression equation of water influx (milliliters per day) on body mass (in grams) was $\text{Water influx} = 0.352 m_b + 5.221$ ($n = 65$; $S_b = 0.06$; $S_{y,x} = 3.56$; $r^2 = 0.36$; and $P < 0.001$), and water efflux (milliliters per day) on body mass (in grams) was $\text{Water efflux} = 0.490 m_b - 2.051$ ($n = 65$; $S_b = 0.05$; $S_{y,x} = 2.99$; $r^2 = 0.61$; and $P < 0.001$, Fig. 3). Water efflux at 22.8 ml/day equalled water influx and this occurred at ~ 50 g body mass. Field metabolic rate (FMR) of the nestlings increased linearly with body mass (Fig. 4). The regression equation of FMR (kilojoules per day) on body mass (in grams) was $\text{FMR} = 1.52 m_b - 4.35$ ($n = 57$; $S_b = 0.37$; $S_{y,x} = 19.12$; $r^2 = 0.24$; and $P < 0.001$).

Discussion.—Arabian Babblers attain adult body mass between 8 and 12 months of age (A. Anava unpubl. data). The nestling phase (12 to 14 days) is short compared to other passerines of similar body mass and to passerines in general (Ricklefs 1968). Shortening the nestling period can (1) allow adults to produce more clutches per year; (2) reduce the risk

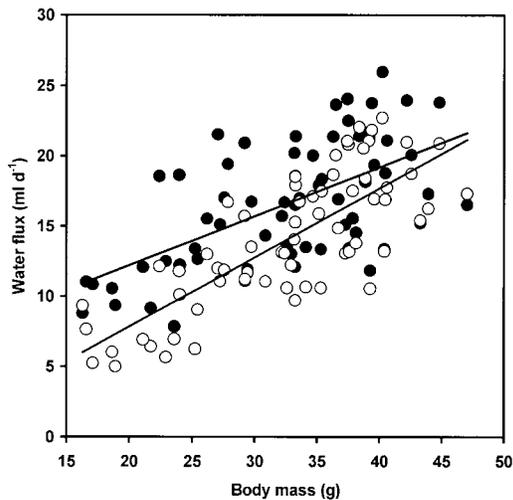


FIG. 3. The effect of body mass on water influx (solid circles) and water efflux (open circles) in Arabian Babbler nestlings.

of predation (Lack 1968); and (3) allow adults and fledglings to move from the nesting site to forage new patches. During the nestling period of babblers, skeletal development is fast, which is typical of most passerines. However, that is not the case with the development of feathers and body size and, as a result, fledglings are unable to fly and to forage independently for about two months (A. Anava pers. obs.). They are dependent on their parents and helpers for food. Thus, those fledglings are like nestlings, but are outside the nests.

The growth rate constant (k) was 0.450/day which was 18% higher than that predicted (0.381/day) for a passerine of its body mass (Ricklefs 1968). The time required to grow from 10 to 90% of its body mass (t_{10-90}) was 9.76 days which was 17% faster than that predicted (11.4 days) for a passerine of its body mass (Ricklefs 1968). The ratio between the asymptote and adult mass, 0.63, is one of the lowest in passerine species (Bateman and Balda 1973, Degen et al. 1992, Weathers et al. 1990, Woolfenden 1978).

Water content, as a fraction of body mass, decreased with age in babbler nestlings. A reduction has been reported in other birds (Robbins 1983, Rowe 1990) and is related to an accumulation of body lipid in growing nestlings (O'Connor 1977, Robbins 1983). Water efflux and influx increased with body mass in growing nestlings. Near fledging (46 g), mass specific water influx was $46 \text{ ml g}^{-1} \text{ day}^{-1}$ which was similar to the $41 \text{ ml g}^{-1} \text{ day}^{-1}$ found for adults (Anava 2000) and similar to Northern Shrike (*Lanius excubitor*) nestlings near fledging (Degen et al. 1992).

Metabolizable energy intake followed a sigmoidal curve, as has been reported for Northern Shrikes

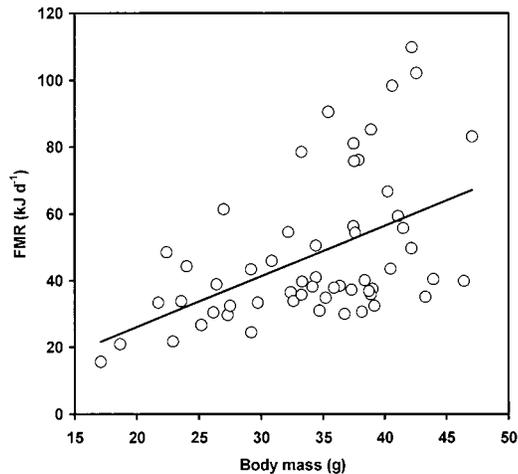


FIG. 4. The effect of body mass on field metabolic rate (FMR) in Arabian Babbler nestlings.

(Degen et al. 1992). It increased with age (Fig. 5) and reached its peak (72 kJ/day) at 10 days of age. Total metabolizable energy intake (MEI) per chick over the nesting phase of 1 to 14 days was 759.4 kJ. This is only 68.5% of the predicted MEI (kJ/nestling) calculated from an equation generated from fledgling body mass and fledging time (Weathers 1992). The ratio of ER to MEI decreased from 0.62 at 1 day of age to 0.05 at 14 days of age (Appendix). Growing nestlings required more energy for maintenance and

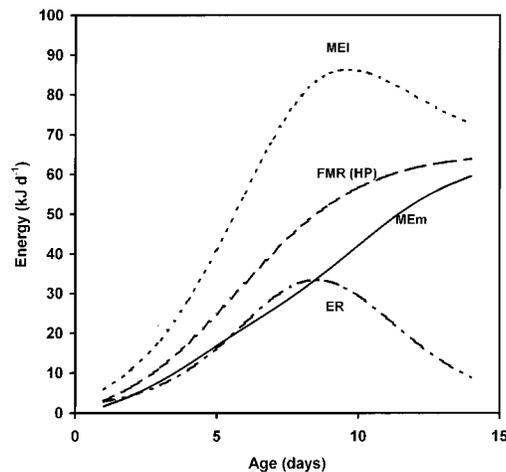


FIG. 5. Metabolizable energy intake (MEI); field metabolic rate (FMR), heat production (HP); metabolizable energy for maintenance (MEM); and energy retention (ER) of Arabian Babbler nestlings. The area between FMR and MEM represents the heat increment of feeding for growth. Values were based on logistic growth curve (see text).

thermoregulation and, therefore, a smaller proportion of MEI was available for growth. Thus, even if the efficiency of utilization of energy for growth remained constant, that is, the relative proportions of heat increment of feeding for growth and of ER stayed constant, the ratio of ER to MEI would decrease. However, concomitantly, as nestlings grew, the ratio of ER per change in body mass increased from 3.18 kJ per g body mass in nestlings of 1 day to 5.65 kJ per g body mass in nestlings of 14 days. The nestlings were putting on proportionately more body solid and more lipid as they grew, and thus the energy content per change in body mass increased with age. Average energy content per gram of body mass over the whole nestling period was 4.48 kJ per gram.

Calculated total dry matter and fresh matter intakes of each young over the 14 day nestling period was 35.8 and 202.3 g, respectively. Mass-specific daily dry matter intake generally decreased with age and ranged between 0.07 and 0.11 per gram of body mass. Lowest fresh-matter intake per day as a fraction of body mass was 0.52 at 12 to 14 days of age and highest fresh-matter intake as a fraction of body mass per day was 1.49 on the day after hatching. Red-backed Shrikes (*Lanius collurio*) had an overall fresh-matter intake per day of 0.56 body mass with a daily range of 0.40 to 0.78 (Diehl 1971) and Northern Shrikes had a daily intake of 0.38 to 0.85 of body mass.

We concluded that our hypothesis was partially confirmed. Growth rate of Arabian Babbler nestlings was relatively fast compared to other passerine species, but fledging mass was relatively low. A consequence of early fledging could be that predation is reduced and foraging area in a harsh environment is increased.

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LITERATURE CITED

- ANAVA, A., M. KAM, A. SHKOLNIK, AND A. A. DEGEN. 2000. Seasonal field metabolic rate and dietary intake in Arabian Babblers (*Turdoides squamiceps*) inhabiting extreme deserts. *Functional Ecology* 14:607–613.
- BATEMAN, G. C., AND R. P. BALDA. 1973. Growth, development, and food habits of young Pinon Jays. *Auk* 90:39–61.
- DEGEN, A. A., B. PINSHOW, P. U. ALKON, AND H. ARNON. 1981. Tritiated water for estimating total body water and water turnover rate in birds. *Journal of Applied Physiology: Respiratory, Environmental and Exercise Physiology* 51:1183–1188.
- DEGEN, A. A., B. PINSHOW, R. YOSEF, M. KAM, AND K. A. NAGY. 1992. Energetics and growth rate of Northern Shrike (*Lanius excubitor*) nestlings. *Ecology* 73:2273–2283.
- DIEHL, B. 1971. Productivity investigation of two types of meadows in the Vistula Valley. XII. Energy requirement in nestling and fledgling Red-backed Shrike (*Lanius collurio* L.). *Ekologia Polska* 19:235–248.
- EVENARI, M., L. SHANAN, AND N. TADMOR. 1982. *The Negev: The Challenge of a Desert*, 2nd ed. Harvard University Press, Cambridge, Massachusetts.
- LACK, D. 1968. *Ecological Adaptation for Breeding in Birds*. Methuen, London.
- NAGY, K. A. 1980. CO₂ production in animals: Analysis of potential errors in the doubly labeled water method. *American Journal of Physiology* 238: R466–R473.
- NAGY, K. A. 1983. The doubly labeled water (³HH¹⁸O) method: A guide to its use. UCLA Publication Number 12–1417, University of California at Los Angeles, Los Angeles.
- O'CONNOR, R. J. 1977. Differential growth and body composition in altricial passerines. *Ibis* 119:147–166.
- RICKLEFS, R. E. 1968. Patterns of growth in birds. *Ibis* 110:419–451.
- ROBBINS, C. R. 1983. *Wildlife Feeding and Nutrition*. Academic Press, New York.
- ROWE, R. A. 1990. Tritiated water measurements of water flux in nestling and adult Zebra Finches (*Poephila guttata*). *Comparative Biochemistry and Physiology* 95A:253–257.
- STERN, E., Y. GRADUS, A. MEIR, S. KRAKOVER, AND H. TSOAR. 1986. *Atlas of the Negev*. Keterpress Enterprises, Jerusalem, Israel.
- UNITED NATIONS EDUCATIONAL, SCIENTIFIC AND CULTURAL ORGANIZATION. 1977. Map of the world distribution of arid lands. MAB, Technical Note 7. UNESCO, Paris.
- WEATHERS, W. W. 1992. Scaling nestling energy requirements. *Ibis* 134:142–153.
- WEATHERS, W. W., M. T. STANBACK, AND W. D. KOENIG. 1990. Breeding energetics and thermal ecology of the Acorn Woodpecker in central coastal California. *Condor* 92:341–359.
- WEATHERS, W. W., AND K. A. SULLIVAN. 1991. Growth and energetics of nestling Yellow-eyed Juncos. *Condor* 93:138–146.
- WOOD, R. A., K. A. NAGY, S. T. MACDONALD, S. I. WAKAKUWA, R. J. BECKMAN, AND H. KAAZ. 1975. Determination of oxygen-18 in water contained in biological samples by charged particle activation. *Analytical Chemistry* 47:646–650.
- WOOLFENDEN, G. E. 1978. Growth and survival of young Florida Scrub Jays. *Wilson Bulletin* 90:1–18.

- WRIGHT, J. 1997. Helping-at-the-nest in Arabian Babblers: Signalling social status or sensible investment in chicks? *Animal Behaviour* 54:1439–1448.
- WRIGHT, J. 1998. Helping-at-the-nest and group size in the Arabian Babblers (*Turdoides squamiceps*). *Journal of Avian Biology* 29:105–112.
- ZAHAVI, A. 1989. Arabian Babbler. Pages 253–275 in *Lifetime Reproduction in Birds* (I. Newton, Ed.). Academic Press, London.
- ZAHAVI, A. 1990. Arabian Babblers: The quest for social status in a cooperative breeder. Pages 105–130 in *Cooperative Breeding in Birds* (P. B. Stacey and W. D. Koenig, Eds.). Cambridge University Press, Cambridge, United Kingdom.

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APPENDIX. Parameters of the nestling Arabian Babbler's energy budget.

Age (d)	m_b^a (g)	Δm_b (g)	ER ^b (kJ/day)	FMR ^c (kJ/day)	MEI ^d (kJ/day)	ER/MEI
0	3.22	0.00	0.00	3.14		
1	4.86	1.64	5.21	3.16	8.37	0.622
2	7.19	2.33	7.74	6.58	14.32	0.540
3	10.36	3.17	11.13	11.40	22.53	0.494
4	14.40	4.04	15.23	17.54	32.77	0.465
5	19.18	4.77	19.38	24.80	44.18	0.439
6	24.32	5.14	22.49	32.61	55.10	0.408
7	29.32	5.01	23.48	40.22	63.70	0.369
8	33.76	4.43	22.00	46.96	68.96	0.319
9	37.36	3.60	18.67	52.44	71.11	0.263
10	40.09	2.73	14.60	56.59	71.19	0.205
11	42.05	1.96	10.71	59.56	70.28	0.152
12	43.40	1.35	7.51	61.62	69.12	0.109
13	44.31	0.91	5.10	63.00	68.09	0.075
14	44.91	0.60	3.38	63.91	67.29	0.050
Total		41.7	219.1	543.5	759.4	0.289

^a Mean body mass (m_b ; gram) = $46 / [(1 + 13.27) \times e^{-0.45 \times t}]$.

^b Daily energy retention (ER) calculated as: ER = fraction of body solids $\times \Delta m_b \times$ energy yield. ER = $(1 - (0.865 - 0.0029 \times m_b)) \times \Delta m_b \times 21.3$.

^c Field metabolic rate calculated from the equation: FMR = $1.52 \times m_b^{-1.35}$.

^d Metabolizable energy intake: MEI = FMR + ER.

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Does Group Size Affect Field Metabolic Rate of Arabian Babbler (*Turdoides squamiceps*) Nestlings?

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ABSTRACT.—Arabian Babblers (*Turdoides squamiceps*) are territorial, cooperative breeding passerines in which groups consist of parents and helpers. All members of the group feed nestlings in a single nest and all group members provision at similar rates. We hypothesized that the field metabolic rate (FMR) of Arabian Babbler nestlings is related to group feeding; that is, FMR would be greater in nestlings of larger rather than smaller sized groups. To test that hypothesis, we measured FMR of 10 day old nestlings from small (2 and 3 individuals), medium (4 and 5 individuals), and large (6 or more individuals) groups. We also determined number of hatchlings and fledglings produced per group. There was an increase in body mass and FMR from small to medium-sized groups, but there was a levelling off or decrease in those parameters in large groups. That suggests that there is an optimum group number for provisioning nestlings, above which there may be a negative effect. The relationship between group size and annual number of eggs was not significant, but there was a positive and linear relationship between group size and annual fledglings production. Thus, more eggs reached the fledgling stage with an increase in group size, suggesting that larger groups are better able to defend the nest against predators.

There are over 200 species of cooperative breeding birds in which parents and helpers feed nestlings (Brown 1987). Group size varies within species, and the significance of the number of individuals has been researched and discussed extensively (Wright 1998, Shaw and Shewry 2000). It has been suggested that because helpers provision nestlings, they can increase the productivity of the group. Helpers can reduce the onus placed on parents to provision nestlings and reduce the parents' reproduction costs (Rabenold 1990, Sydesman 1989), which can allow the parents to nest more frequently and produce more offspring.

The Old World genus *Turdoides* includes 29 species. Of these babbler species, 14 are known to be cooperative breeders and 12 are likely to be so (see Shaw

and Shewry 2000). Territories are usually passed through the males, whereas the females disperse more readily (Gaston 1978a, Shaw and Shewry 2000). The Arabian Babbler (*T. squamiceps*) inhabits extreme deserts and is the only bird species in Israel that lives in groups year round. Those groups are territorial, with number of birds per group generally between 3 and 5 individuals, but can range between 2 and 22. Each group usually contains one breeding pair; young birds do not disperse for one to three years, during which time they act as helpers (Zahavi 1989, 1990). Zahavi (1974, 1990) found either no relationship between group size and number of fledglings produced or, when there was a relationship, it was restricted to smaller groups and to certain years. Wright (1998), studying babblers at the same site over a three year period, found that larger groups produced more fledglings.

Arabian Babbler helpers and parents provision nestlings at similar rates, irrespective of sex or dominance rank within the group (Wright 1997, 1998). Consequently, nestlings from large groups should receive more food than nestlings from small groups. We hypothesized, therefore, that group size has an effect on the field metabolic rate (FMR) of nestlings; that is, field metabolic rate would be greater with an increase in group size. To test that hypothesis, we determined FMR and body mass of nestlings from different sized Arabian Babbler groups. We also determined the number of nestlings and fledglings produced by the groups.

Materials and Methods.—*Study species and study site.*—We divided the groups of babblers into three size categories: *small* included 2 and 3 individuals, *medium* included 4 and 5 individuals, and *large* included 6 or more individuals. The study was done from January 1994 to December 1995 at the Nature Reserve at Hatzeva (30°45'N, 35°15'E) in the Arava, ~30 km south of the Dead Sea. The Arabian Babbler and the site have been described (Anava et al. 2001).

Doubly labelled water measurements.—Measurements of FMR and water flux on 10 day old Arabian Babbler nestlings were done as described by Anava et al. (2001). Only one nestling, chosen at random, was measured per nest.

Treatment of data.—The study was done over two breeding seasons on 36 groups. We collected data on

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TABLE 1. Water efflux, field metabolic rate and body mass of 10 day old nestling babblers from small (2–3 adults), medium (4–5 adults) and large (6–9 adults) groups. Values are means \pm SD. Values within rows with different superscripts are different from each other ($P < 0.05$).

Group size	Small	Medium	Large
Sample size	14	24	20
Body mass (g)	35.9 \pm 1.54 ^a	39.8 \pm 1.24 ^b	38.7 \pm 2.18 ^{ab}
Water efflux (ml/d)	13.6 \pm 1.18 ^a	15.9 \pm 0.95 ^b	14.5 \pm 0.90 ^{ab}
Field metabolic rate (kJ/d)	43.3 \pm 6.53 ^a	59.6 \pm 5.6 ^b	46.1 \pm 5.13 ^a

each group each year and treated the data on groups as statistically independent ($n = 72$). That seemed justified because the helpers and composition of some of the groups as well as the group size changed between years. There were 20 small, 31 medium, and 21 large groups. We used a two-way analysis of covariance (ANCOVA) to analyze for difference of body mass among group sizes, taking brood size as a covariate factor. In that way, the effect of brood size on body mass of the nestlings was removed. In addition, we used a two-way ANCOVA to analyze for difference of FMR and water flux among group sizes, taking body mass and brood sizes as covariate factors. Thus, the effects of body mass and brood size on water flux and FMR were removed. Least squares difference (LSD) was used to separate means where significance was found. Data are presented as means \pm 1 SD, and $P < 0.05$ was chosen as the lowest acceptable level of significance.

Results.—Nestling development, growth, water flux and field metabolic rate.—At 10 days of age, nestlings from medium-sized groups had a greater body mass ($P < 0.04$) than nestlings from small groups; large groups did not differ from either small or medium-sized groups (Table 1). FMR of 10 day old nestlings from medium-sized groups was higher ($P < 0.05$) than that of small and large groups (Table 1). Water efflux of 10 day old nestlings from medium-sized groups tended to be higher ($P < 0.07$) than that of small and large groups (Table 1).

Reproductive success.—Group size did not have a significant relationship with annual number of eggs

(Table 2). However, the relationship between the annual number of fledglings (N_f) and group size (GS) was significant and took the form (Fig. 1):

$$N_f = 0.316 + 0.0805 \text{ GS}$$

($n = 72$; $S_a = 0.89$ $S_b = 0.18$; $S_{y,x} = 2.69$; $F = 19.7$, $df = 1$ and 70 ; $r^2 = 0.22$ and $P < 0.001$).

Of 169 total nesting attempts, 34.9% (59 of 169) failed to produce fledglings. Small groups failed in 43% (20 of 46), medium-sized groups in 37% (30 of 81), and large groups in 21% (9 of 42) of nest attempts.

Discussion.—Body mass and field metabolic rate.—In some species of cooperative breeding birds, growth rate of nestlings is higher with more helpers (Bennun 1994), but that was not found for all communal birds (Brown 1987, Dow and Wilmore 1990). Wright (1998) found no relationship between group size and body mass in 10 day old Arabian Babbler nestlings. However, in this study, body mass of 10 day old nestlings from medium-sized groups was greater than that of small groups and, therefore, group size had an effect on body mass. But body mass did not increase with group size in large groups. In fact, nestlings from the medium-sized groups tended to have the greatest body mass.

FMR in 10 day old nestlings basically followed the same relationship to group size as did body mass; that is, FMR was highest in nestlings attended by medium-sized groups. That indicates that the nestlings from the medium-sized groups received the most food and energy and explains the difference in body

TABLE 2. Annual reproductive characteristics and success in Arabian Babblers of different group sizes. Values are means \pm SD. Values within columns with different superscripts are different from each other (ANCOVA, $P < 0.05$).

Group size	n	Number of nesting attempts					
			Eggs	Hatchlings	Nestlings	Fledglings	Fledglings/eggs
2	7	1.6 \pm 0.5	5.2 \pm 1.8	3.6 \pm 1.5 ^a	3.2 \pm 1.1 ^a	2.4 \pm 0.5 ^a	0.50 \pm 0.18 ^{ab}
3	13	2.2 \pm 1.1	8.3 \pm 3.9	5.6 \pm 2.8 ^{ab}	4.8 \pm 2.2 ^{ab}	3.0 \pm 2.0 ^{ab}	0.36 \pm 0.20 ^a
4	22	2.4 \pm 0.9	8.6 \pm 3.3	5.2 \pm 1.9 ^{ab}	5.0 \pm 2.0 ^{abc}	4.0 \pm 2.2 ^{ab}	0.51 \pm 0.31 ^{ab}
5	9	2.2 \pm 1.0	9.1 \pm 3.7	6.8 \pm 2.3 ^{bc}	6.0 \pm 2.3 ^{bd}	5.0 \pm 2.7 ^{abc}	0.60 \pm 0.29 ^{ab}
6	8	2.3 \pm 1.0	7.8 \pm 2.6	7.3 \pm 2.5 ^{bc}	5.8 \pm 3.9 ^{abcd}	5.5 \pm 4.1 ^{abc}	0.68 \pm 0.39 ^{ab}
7	4	2.7 \pm 1.2	9.7 \pm 3.8	8.3 \pm 4.1 ^c	8.3 \pm 4.1 ^d	6.7 \pm 4.9 ^c	0.59 \pm 0.37 ^{ab}
8	6	2.3 \pm 0.6	9.3 \pm 2.3	7.7 \pm 0.6 ^{bc}	7.3 \pm 1.2 ^{cd}	7.3 \pm 1.2 ^c	0.81 \pm 0.17 ^b
9	3	2.7 \pm 1.2	10.3 \pm 4.0	8.0 \pm 0.0 ^{bc}	7.7 \pm 0.6 ^{bc}	6.3 \pm 1.5 ^{abc}	0.68 \pm 0.30 ^{ab}

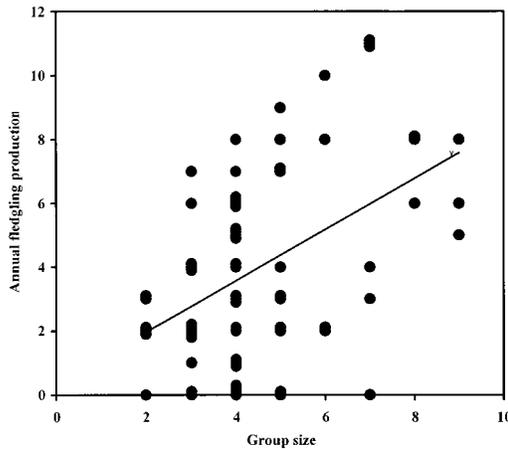


FIG. 1. The relationship between group size and the annual production of Arabian Babbler fledglings.

mass of nestlings among group sizes. FMR is composed of maintenance heat production and the heat increment of feeding for growth, but does not include energy retained in the body (Kam and Degen 1997a, b). Because the nestlings of medium-sized groups were largest, then those nestlings had a higher heat increment of feeding for growth than nestlings from small and large groups, and that could explain, at least in part, the higher FMR in those nestlings.

Reproductive success: Group size effect.—The effect of helpers on reproductive success has been discussed widely, and several theories in relation to nestling survival and body size have emerged: (1) more helpers improve the survival of nestlings by antipredator behavior (Mumme 1992, Woolfenden 1980); (2) more helpers bring more food, and therefore chick mortality due to starvation will be reduced, and growth rate will increase (Bennun 1994); and (3) allofeeding with more helpers will put less onus on the parents to provide food allowing the parents to reduce the interval between broods and produce more offspring per year.

In general, groups with helpers are more successful in reproduction than just pairs, and there is an increase in reproductive success with an increase in number of helpers. For example, Colonial Bee-eaters (*Merops bullockoides*) with helpers have more clutches and lower nestling mortality than just pairs (Dyer and Fry 1980). In addition, pairs with two to three helpers are twice as successful as pairs without helpers (Emlen et al. 1980). Florida Scrub Jays (*Aphelocoma coerulescens*) with one to four helpers have 2.1 offspring, whereas pairs without helpers have only 1.2 offspring per year (Woolfenden 1980). Similar results were found for *Campylorhynchus* wrens. Groups of those wrens usually range between two to eight in-

dividuals (pair plus zero to six helpers). Without helpers, reproductive success is extremely low; however, with two helpers (four individuals), there is a dramatic increase in reproductive success. Increases in number of helpers above that number results in only moderate increases in reproductive success (Rabenold 1990). However, benefits have not always been reported for cooperative breeders (Brown 1987). No effect on breeding success per nest because of helpers was found in the Superb Fairy-wren (*Malurus cyaneus*), in that groups (pair plus helpers) and pairs did not differ in nestlings hatched per egg laid, fledglings produced per hatchlings, number of nesting attempts, and number of fledglings produced per season (Nias and Ford 1992).

Babblers.—No relationship between group size and breeding success was found in the Common Babbler (*Turdoides caudatus*; Gaston 1978a), Jungle Babbler (*Turdoides striatus*; Gaston 1978b), Arrow-marked Babbler (*Turdoides jardineii*; Monadjem et al. 1995) and Bare-cheeked Babbler (*Turdoides gymnogenys*; Shaw and Shewry 2000). Results for the Arabian Babbler have been equivocal. Zahavi (1974), observing Arabian Babblers at Hazeva, first reported no relationship between group size and the number of fledglings produced; however, in a later study (Zahavi 1990), he found that a relationship between group size and fledglings occurred, but it was restricted to small group sizes and only to certain years. Wright (1998), studying Arabian Babblers at the same site as Zahavi, found a positive and linear relationship between group size and the reproductive success of the parents.

Zahavi (1974) theorized that chick feeding by Arabian Babbler helpers acts as a signal by the helper to gain social prestige within the group. Competition for social prestige can cause interference among helpers and can actually have a negative effect on productivity of the group (Carlisle and Zahavi 1986). In this study, there was an increase in body mass and FMR from small to medium-sized groups, but there was a levelling off or decrease in these parameters in large groups. Those results suggest that there is an optimum group number for provisioning nestlings, above which there may be a negative effect. That may be due to interference among the helpers. The relationship between group size and annual egg production was not significant, but there was a positive and linear relationship between group size and annual fledglings production. Highest percentage of nests that did not produce nestlings was in the small groups whereas the lowest percentage was in the large groups. That would indicate more eggs reached the fledgling stage with an increase in group size, suggesting that larger groups are better able to defend the nest against predators.

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LITERATURE CITED

- ANAVA, A., M. KAM, A. SHKOLNIK, AND A. A. DEGEN. 2001. Growth rate and energetics of Arabian Babbler (*Turdoides squamiceps*) nestlings. *Auk* 118:519–524.
- BENNUN, L. 1994. The contribution of helpers to feeding nestlings in Grey-capped Social Weavers, *Pseudonigrita arnaudi*. *Animal Behaviour* 47:1047–1056.
- BROWN, J. L. 1987. *Helping and Communal Breeding in Birds*. Princeton University Press, Princeton, New Jersey.
- CARLISLE, T. R., AND A. ZAHAVI. 1986. Helping at the nest, allofeeding and social status in immature Arabian Babblers. *Behavioural Ecology and Sociobiology* 18:339–351.
- DOW, D. D., AND M. J. WHITMORE. 1990. Noisy Miners. Pages 559–592 in *Cooperative Breeding in Birds* (P. B. Stacey and W. D. Koenig, Eds.). Cambridge University Press, Cambridge, United Kingdom.
- DYER, M., AND C. H. FRY. 1980. The origin and role of helpers in bee-eaters. Pages 862–868 in *Acta XVII Congressus Internationalis Ornithologici* (R. Nöhring, Ed.). Deutsche Ornithologia Gesellschaft, Berlin.
- EMLEN, S. T., N. J. DEMONG, AND R. E. HEGNER. 1980. Bee-eaters: An alternative route to cooperative breeding. Pages 895–901 in *Acta XVII Congressus Internationalis Ornithologici* (R. Nöhring, Ed.). Deutsche Ornithologia Gesellschaft, Berlin.
- GASTON, A. J. 1978a. Ecology of the Common Babbler *Turdoides caudatus*. *Ibis* 120:415–432.
- GASTON, A. J. 1978b. Demography of the Jungle Babbler *Turdoides striatus*. *Journal of Animal Ecology* 47:845–870.
- KAM, M., AND A. A. DEGEN. 1997a. Energy budget in free-living animals: A novel approach based on the doubly-labelled water method. *American Journal of Physiology* 272:R1336–R1343.
- KAM, M., AND A. A. DEGEN. 1997b. Energy requirements and the efficiency of utilization of metabolizable energy in free-living animals: Evaluation of existing theories and generation of a new model. *Journal of Theoretical Biology* 184:101–104.
- MONADJEM, A., N. OWEN-SMITH, AND A. C. KEMP. 1995. Aspects of the breeding biology of the Arrowmarked Babbler *Turdoides jardineii* in South Africa. *Ibis* 137:515–518.
- MUMME, R. L. 1992. Do helpers increase reproductive success? An experimental analysis in the Florida Scrub Jay. *Behavioural Ecology and Sociobiology* 31:319–328.
- NIAS, R. C., AND H. A. FORD. 1992. The influence of group size and habitat on reproductive success in the Superb Fairy-wren *Malurus cyaneus*. *Emu* 92:238–243.
- RABENOLD, K. N. 1990. *Campylorhynchus* wrens: The ecology and delayed dispersal and cooperation in the Venezuela savanna. Pages 159–196 in *Cooperative Breeding in Birds* (P. B. Stacey and W. D. Koenig, Eds.). Cambridge University Press, Cambridge, United Kingdom.
- SHAW, P., AND M. SHEWRY. 2000. Abundance, group size and breeding success of Bare-cheeked Babblers *Turdoides gymnogenys*. *Ibis* 142:58–64.
- SYDEMAN, W. J. 1989. Effects of helpers on nestling care and breeder survival in Pygmy Nuthatches. *Condor* 91:147–155.
- WOOLFENDEN, G. E. 1980. Selfish behavior of avian altruists. Pages 886–889 in *Acta XVII Congressus Internationalis Ornithologici* (R. Nöhring, Ed.). Deutsche Ornithologia Gesellschaft, Berlin.
- WRIGHT, J. 1997. Helping-at-the-nest in Arabian Babblers: Signalling social status or sensible investment in chicks? *Animal Behaviour* 54:1439–1448.
- WRIGHT, J. 1998. Helping-at-the-nest and group size in the Arabian Babblers (*Turdoides squamiceps*). *Journal of Avian Biology* 29:105–112.
- ZAHAVI, A. 1974. Communal nesting by the Arabian Babbler: A case of individual selection. *Ibis* 116:84–87.
- ZAHAVI, A. 1989. Arabian Babbler. Pages 253–275 in *Lifetime Reproduction in Birds* (I. Newton, Ed.). Academic Press, London.
- ZAHAVI, A. 1990. Arabian Babblers: The quest for social status in a cooperative breeder. Pages 105–130 in *Cooperative Breeding in Birds* (P. B. Stacey and W. D. Koenig, Eds.). Cambridge University Press, Cambridge, United Kingdom.

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