when food was scarce. Hansen (1986) also equated instances of talon-to-body contact with relative scarcity of food. He found 4.5% of the interactions included contact during food scarcity, while only 0.6% included contact when food was abundant. Hunger was likely the driving factor causing the increased aggression exhibited by eagles during food scarcity. In this study, one male used contact in an interaction against a female of the same age after the male had been away from the hacking platform for 16 days; the male had been followed closely by telemetry and was not known to have fed during that period.

In this study, size appears to be the most important factor in determining the outcome of an interaction. While age (as displayed by plumage) may be used by eagles to evaluate the potential fighting ability of opponents, it may not be as important as size. Knight and Skagen (1988) found that the probability of a small eagle supplanting any other eagle was low unless a small adult was attempting to pirate from a small immature. Other factors, such as hunger level (Hansen 1986), may act as modifiers which alter the risk/benefit associated with challenging a potentially more dangerous (i.e., larger and/or older) opponent.

I would like to thank Gary Roemer, Richard Golightly, David Kitchen, Debra Schlafmann, and two anonymous reviewers for their comments on the manuscript.

LITERATURE CITED

Anderson, D. J., and R. J. Horwitz. 1979. Competitive interactions among vultures and their avian competitors. Ibis 121:505–509.

Garcelon, D. K. 1988. The reintroduction of bald eagles on Santa Catalina Island, California. M.Sc.thesis, Humboldt State Univ., Arcata, CA.

Garcelon, D. K., M. S. Martell, P. T. Redig, and L. C. Buoen. 1985. Morphometric, karyotypic, and laparoscopic techniques for determining sex in bald eagles. J. Wildl. Manage. 49:595–599.

Griffin, C. R. 1981. Interactive behavior among Bald Eagles wintering in north-central Missouri. Wilson Bull. 93:259–264.

Hansen, A. J. 1986. Fighting behavior in bald eagles: A test of game theory. Ecology 67:787–797.

Knight, R. L., and S. K. Knight. 1983. Aspects of food finding by wintering Bald Eagles. Auk 100: 477–484.

Knight, R. L., and S. K. Skagen. 1988. Agonistic asymmetries and the foraging ecology of bald eagles. Ecology 69:1188–1194.

McClelland, B. R. 1973. Autumn concentrations of Bald Eagles in Glacier National Park. Condor 75:121–123.

Petrides, G. A. 1959. Competition for food between five species of east African vultures. Auk 76:104–106.

Sherrod, S. K., C. M. White, and F.S.L. Williamson. 1977. Biology of the Bald Eagle on Amchitka Island, Alaska. Living Bird 15:143–182.

Stalmaster, M. V. 1976. Winter ecology and effects of human activity on bald eagles in the Nooksack River Valley, Washington. M.Sc.thesis, Western Washington State College, Bellingham.

Stalmaster, M. V., and J. A. Gessaman. 1984. Ecological energetics and foraging behavior of overwintering bald eagles. Ecol. Monogr. 54:407–428.

Wallace, M. P., and S. A. Temple. 1987. Competitive interactions within and between species in a guild of avian scavengers. Auk 104:290–295.

The Condor 92:534–537

CLUTCH SIZE, OFFSPRING QUALITY, AND FEMALE SURVIVAL IN TREE SWALLOWS—AN EXPERIMENT[1]

David A. Wiggins
Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, V5A 1S6 Canada

Key words: Tree Swallow; Tachycineta bicolor; *clutch size; adult survival; offspring size.*

Many proximate factors, such as time of season, geographical location, and the age of the female are known to affect clutch size in birds (Klomp 1970, Murphy and Haukioja 1986). From an ultimate perspective, Lack's (1947, 1966, 1968) viewpoint, that individuals set their clutch size to the level that produces the maximal number of offspring contributed to the next generation, has recently been modified to account for annual fluctuations in environmental conditions (Van Noordwijk et al. 1981, Boyce and Perrins 1987). While some authors have argued that a cost of reproduction, via adult survival, has acted as the major constraint on clutch size (Williams 1966, Charnov and Krebs 1974), several recent studies have provided no evidence of such costs (De Steven 1980, Smith 1981, Boyce and Perrins 1987,

---

[1] Received 7 September 1989. Final acceptance 15 December 1989.

TABLE 1. Clutch size, day 16 brood size, nestling mass, and nestling tarsus length of expanded, control, and reduced Tree Swallow broods. Sample sizes refer to the number of broods in each treatment group. Brood means were used to compare nestling mass and tarsus length.

		Clutch size		Brood size		Body mass		Tarsus length	
	n	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Expanded	8	5.9^{a}	0.3	7.3^{b}	0.7	18.27^{c}	1.54	10.3^{e}	0.5
Control	13	5.7	0.5	5.3	0.7	21.16^{d}	1.33	10.5	0.4
Reduced	8	5.9	0.3	3.5	0.5	20.53	1.09	10.1	0.5

[a] Expanded = control = reduced, Kruskal-Wallis test = 0.69, $P > 0.05$.
[b] Expanded > control > reduced, Kruskal-Wallis test = 22.4, $P < 0.0001$.
[c] Expanded < control, Mann-Whitney $U = 12$, $P < 0.01$; Expanded < reduced, Mann-Whitney $U = 7$, $P < 0.01$.
[d] Control = reduced, Mann-Whitney $U = 35.5$, $P > 0.05$.
[e] Expanded = control = reduced, Kruskal-Wallis test = 4.26, $P > 0.05$.

Gustafsson and Sutherland 1988, Pettifor et al. 1988, Alatalo and Lundberg 1989).

Another potential constraint on clutch size involves the trade-off between clutch size and offspring survival and/or quality (Lack 1954, Perrins and Moss 1975, Pettifor et al. 1988). Several studies have shown that artificial increases in brood size result in lower fledgling mass (Askenmo 1977; Nur 1984a; Gustafsson, unpubl. data cited in Gustafsson and Sutherland 1988, Alatalo and Lundberg 1989). As it is often correlated with subsequent juvenile survival (Perrins 1965, Garnett 1981, Gustafsson and Sutherland 1988, but see Nur 1984a), fledgling mass may provide a reliable indication of the probability of recruitment to the breeding population. In this study, I manipulated the brood size of Tree Swallows (*Tachycineta bicolor*) and monitored both the reproductive success and overwinter survival of females raising enlarged, reduced, and control broods.

STUDY AREA AND METHODS

Data were collected from early May to early July 1987 at the Creston Valley Wildlife Management Area in southeastern British Columbia. Details of the study site and of measurements taken on nestlings are described elsewhere (Wiggins 1989). Nests used for experimental chick transfers were chosen opportunistically due to limited breeding synchrony. Unmanipulated nests were used as controls. Experimental nests were paired according to clutch size and hatching date. Two 1- to 2-day-old young were removed from each "reduced" brood and placed in their paired "expanded" brood. Nests were checked two or three times/day near hatching to determine nestling age. All young transferred between broods were similar in age (to within 12–14 hr) to their foster broodmates.

Initially, 28 nests (22 six-egg clutches, six five-egg clutches) were manipulated. However, predation of females and/or nestlings reduced the number of experimental broods to 23. In addition, nests used in the analysis were restricted to those in which a maximum of one chick was lost during the nestling stage. Thus, only those expanded nests in which brood size was at least clutch size + 1 were included in the analyses. Four expanded and three reduced broods were excluded due to the loss of two or more nestlings.

Nestling mass and tarsus length in the three treatment groups were measured 16 days after hatching and were analyzed by comparison of brood means. While this analysis neglected within-brood sources of variation, it was useful in this study as the three treatment groups each contained a range of brood sizes (reduced: three to four nestlings; control: five to six nestlings; expanded: seven to eight nestlings).

All breeding females were captured on the nest during incubation and banded with plastic color bands and with U.S. Fish and Wildlife Service aluminum bands. Survivorship estimates were derived from recaptures and sightings of females in 1988. Survivorship rates were minimum estimates as emigration to other breeding sites may have occasionally occurred—four of the approximately 170 breeding females banded in 1986 and 1987 skipped breeding in the study area and returned to breed in subsequent years.

RESULTS AND DISCUSSION

The clutch size, day 16 brood size, nestling mass, and tarsus length of the three groups are presented in Table 1. Clutch size did not differ significantly between the three groups. However, there was a significant difference in brood size at day 16 with expanded broods > control broods > reduced broods. The mean differences between the number of young at day 16 and the initial clutch sizes were +1.37 (expanded broods), −0.38 (control broods), and −2.38 (reduced broods). These differences were due to unhatched eggs ($n = 6$) and apparent nestling starvation ($n = 6$, including four in expanded broods). The mean nestling mass in expanded broods was significantly lower than that of nestlings in both control and reduced broods. Tarsus length did not differ between the three groups.

The return rate of breeding females was calculated for each group. The return rates of females raising enlarged broods (5/8, 63%) did not differ from that of females raising either control (5/13, 38%) or reduced (3/8, 38%) broods ($G = 0.49$, $P > 0.05$).

The experiment was successful in establishing significant differences in brood size among the three treatment groups at day 16. However, there was no significant difference between reduced and control broods in the mass of nestlings. Conversely, expanded broods showed significantly lower nestling masses at day 16 than either control or reduced broods. Alatalo and Lundberg (1989) found that experimentally reduced Pied Flycatcher (*Ficedula hypoleuca*) broods produced significantly heavier nestlings than controls, whereas enlarged broods produced significantly lighter nestlings. However, in another study of Pied Flycatchers, Askenmo (1977) found that brood size manipulations had significant effects on nestling mass during only 1 of 2 years. Thus, environmental conditions at the time of breeding appear to have an impact on fledgling mass. In addition, De Steven (1980) showed that manipulated brood size had no effect on the mass of nestling Tree Swallows raised by old females, and only small effects on the mass of nestlings raised by first-year females. As only six (three reduced, two expanded, one control) of the 29 females in my study were first-year birds, female age likely had negligible, if any, effects.

Nestling mass at fledging has been shown to affect the subsequent probability of survival in a number of passerine species (Great Tits *Parus major,* Perrins 1965, Garnett 1981; Blue Tits *P. caeruleus,* Nur 1984a; Pied Flycatcher and Collared Flycatcher *Ficedula albicollis,* Alatalo and Lundberg 1989). De Steven (1978) found no effects of brood-size manipulation on the subsequent return rates of juvenile Tree Swallows in southern Ontario. However, this was not surprising as the manipulations had no effect on the mass of nestlings, relative to brood size (De Steven 1980). Low return rates (1–2% annually) of juveniles precluded such analyses in the Creston Tree Swallow population.

Alatalo and Lundberg (1989) used the survival probabilities of fledgling Collared Flycatchers (Gustafsson, unpubl. data) to estimate recruitment rate in their population of Pied Flycatchers. If Gustafsson's estimates of recruitment probabilities are applicable to other small, hole-nesting, aerial insectivores, then Tree Swallow fledglings from my expanded broods likely realized poor recruitment. Gustafsson found that fledgling in the range of 87–93% of the mean fledgling mass for the population returned to the breeding area at only 20% of the frequency of heavier nestlings. In my study, fledglings from expanded broods were 10% lower than the mean mass of fledglings in the population. Consequently, normal-sized broods likely produced the greatest number of recruits to the breeding population (cf. Hogstedt 1980).

The effects of a cost to reproduction on adult survival may be small and, consequently, require large data sets to detect (cf. Gustafsson and Sutherland 1988, Pettifor et al. 1988, Alatalo and Lundberg 1989). Although the sample sizes in my study were small, there was no indication that females raising enlarged broods had lower return rates the following spring. However, small sample sizes severely restricted the statistical power in such comparisons and the results should be viewed as tentative at best.

While the results of this study represent only one breeding season, they do indicate that offspring quality mediated through brood size may constrain clutch size in female Tree Swallows, at least in some years. Alatalo and Lundberg (1989) found that expanded and control Pied Flycatcher broods realized similar recruitment rates, whereas Nur (1984b) found that artificially expanded Blue Tit broods realized higher recruitment rates. Although my single-year data set does not address this point, van Noordwijk et al. (1981) and Boyce and Perrins (1987) suggest that interyear variation in the survival probabilities of both fledglings and adults is likely to produce such varying results.

I thank B. Beasley, J. Karagatzides, L. Schalla, and J. Siderius for help with the fieldwork. The staff of the Creston Valley Wildlife Management Area provided assistance throughout the study. I also thank J. Smith, N. Verbeek, and R. Ydenberg for help in designing the study, and two anonymous reviewers for helpful comments on the manuscript. Financial support for the study was provided by a Grant-in-Aid of Research from Sigma Xi, Simon Fraser University Graduate Research Fellowships, and by a grant from the Natural Sciences and Engineering Research Council of Canada (to N. Verbeek).

LITERATURE CITED

ALATALO, R. V., AND A. LUNDBERG. 1989. Clutch size of the Pied Flycatcher *Ficedula hypoleuca*—an experiment. Ornis Fenn. 66:15–23.

ASKENMO, C. 1977. Effects of addition and removal of nestlings on nestling weight, nestling survival, and female weight loss in the Pied Flycatcher *Ficedula hypoleuca* (Pallas). Ornis Scand. 8:1–8.

BOYCE, M. S., AND C. M. PERRINS. 1987. Optimizing great tit clutch size in a fluctuating environment. Ecology 68:142–153.

CHARNOV, E. L., AND J. R. KREBS. 1974. On clutch size and fitness. Ibis 116:217–219.

DE STEVEN, D. 1978. The influence of age on the breeding biology of the Tree Swallow *Iridoprocne bicolor.* Ibis 120:516–523.

DE STEVEN, D. 1980. Clutch size, breeding success, and parental survival in the tree swallow (*Iridoprocne bicolor*). Evolution 34:278–291.

GARNETT, M. C. 1981. Body size, its heritability and influence on juvenile survival among Great Tits *Parus major.* Ibis 123:31–41.

GUSTAFSSON, L., AND W. J. SUTHERLAND. 1988. The costs of reproduction in the collared flycatcher *Ficedula albicollis.* Nature 335:813–817.

HÖGSTEDT, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. Science 210:1148–1150.

KLOMP, H. 1970. The determination of clutch size in birds: a review. Ardea 58:1–124.

LACK, D. 1947. The significance of clutch-size. Ibis 89:302–352.

LACK, D. 1954. The natural regulation of animal populations. Clarendon Press, Oxford.

LACK, D. 1966. Population studies of birds. Oxford Univ. Press, London.

LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

MURPHY, E. C., AND E. HAUKIOJA. 1986. Clutch size in nidicolous birds, p. 141–180. *In* R. F. Johnston [ed.], Current ornithology. Vol. 4. Plenum Press, New York.

NUR, N. 1984a. The consequence of brood size for breeding blue tits. II. Nestling weight, offspring survival and optimal brood size. J. Anim. Ecol. 53:497–517.

NUR, N. 1984b. The consequences of brood size for breeding blue tits. I. Adult survival, weight change, and the cost of reproduction. J. Anim. Ecol. 53: 479–496.

PERRINS, C. M. 1965. Population fluctuations and clutch size in the great tit *Parus major* L. J. Anim. Ecol. 34:601–647.

PERRINS, C. M., AND D. MOSS. 1975. Reproductive rates in the great tit. J. Anim. Ecol. 44:695–706.

PETTIFOR, R. A., C. M. PERRINS, AND R. H. MCCLEERY. 1988. Individual optimization of clutch size in great tits. Nature 336:160–162.

SMITH, J.N.M. 1981. Does high fecundity reduce survival in song sparrows? Evolution 35:1142–1148.

VAN NOORDWIJK, A. J., J. H. VAN BALEN, AND W. SCHARLOO. 1981. Genetic and environmental variation in clutch size of the great tit. Neth. J. Zool. 31:342–372.

WIGGINS, D. A. 1989. Heritability of body size in cross-fostered tree swallow broods. Evolution 43: 1808–1811.

WILLIAMS, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am. Nat. 100:687–690.

The Condor 92:537

THE CORRECT SPELLING OF *HYPOLEUCUS* REICHENBACH, 1852

DOUGLAS SIEGEL-CAUSEY
Museum of Natural History and Department of Systematics and Ecology,
University of Kansas, Lawrence, KS 66045-2454

By typographic error, I (1988, Condor 90:885–905) used *Hypoleucos* [sic] as a generic name for a clade of mesocormorants. Although this spelling is validly used as a species epithet, the correct usage throughout should be *Hypoleucus* Reichenbach, 1852. In addition, in Appendix 1, state (c) of character #107 should read "lateral scar robust, more than one intervertebral foramen in length." A few minor character-related errors in the figures can be reconciled easily using Appendix 2, which is accurate.

---

[1] Received 15 January 1990. Final acceptance 22 January 1990.