guins within a few days after egg laying. More sophisticated analysis is necessary to sort out individuals with vent sizes in the overlap zones, but individuals of questionable sex can be identified in the field. Once the size ranges for female and male vents have been delineated for a particular species, field researchers can easily sex individual birds to investigate sex-specific behavior and biological patterns that historically have been difficult to study.

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Density Effects on Reproduction of Cavity Nesters in Northern Arizona

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Reproductive success of noncolonial passerines was traditionally thought to decline with increasing intraspecific breeding density. This perception obtained from the classic long-term studies of Great Tits (*Parus major*) in Holland (Kluijver 1951) and England (Lack 1954). More recently, studies of Great Tits and other species have questioned the commonness of negative density effects on fecundity (Tompa 1967, Järvinen 1983, Orell and Ojanen 1983) and the importance of such effects on population dynamics (Perrins 1979, Klomp 1980, van Balen 1980). Data on the frequency of negative density effects are useful for understanding many aspects of avian biology. For example, an assumed inverse density-fecundity relationship underlies certain models of habitat selection and territoriality that relate habitat quality to local conspecific densities (Brown 1969, Fretwell and Lucas 1970). The general applicability of such models is doubtful if negative density-fecundity relationships are not universal. Here I present evidence suggesting that the reproductive success of secondary cavity nesters in northern Arizona is not affected by intraspecific density.

To study density effects, I sought to increase breeding densities of secondary cavity-nesting birds with nest boxes on three 8.0-ha treatment plots (Brawn 1985). The plots were in northern Arizona's ponderosa pine (*Pinus ponderosa*) forests at approximately 2,200 m in the U.S. Forest Service Coconino National Forest, Coconino Co. I installed 60 nest boxes on each plot before the 1980 breeding season (see Brawn and Balda 1983 for details of box installation). All boxes were the same size (approx. volume = 1,900 cm^3).

The treatment plots differed in habitat structure because of silvicultural activity (Szaro and Balda 1979, Brawn and Balda 1983). The Dense treatment plot had not been logged recently and included numerous large, mature pines interspersed with thickets of small

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pine stems. The Thinned treatment plot had been moderately thinned and contained stands of mature and younger "pole-sized" pine interspersed with openings. The Open treatment plot had relatively few trees because of severe thinning.

Boxes promoted increased breeding densities on only the Thinned and Open treatment plots (Brawn and Balda MS); therefore, I could not examine density effects on fecundity on the Dense treatment plot. Three species used boxes in numbers sufficient to examine reproductive output relative to breeding density: Violet-green Swallows (*Tachycineta thalassina*), Pygmy Nuthatches (*Sitta pygmaea*), and Western Bluebirds (*Sialia mexicana*). Data presented here are from 1981-1983. I found only 6 nests in boxes in 1980.

I collected additional data on the reproductive success of Western Bluebirds nesting in natural cavities on a low-density control plot, acknowledging the caveat that breeding success of secondary cavity nesters can be systematically different in nest boxes and natural cavities (Nilsson 1983). Habitat structure on the Control plot was similar to that on the Thinned treatment plot. Inaccessibility of nests in natural cavities prevented treatment-control plot comparisons of Violet-green Swallow and Pygmy Nuthatch reproductive success. I gathered data on the Control plot in 1982 and 1983, subsequent to observation of increasing bluebird densities on the Thinned treatment plot.

I inspected active nests in boxes at least twice weekly throughout each breeding season (late April through late June). Bluebird nests in natural cavities were inspected weekly. For each nest I recorded the date of clutch initiation (estimated by "back-dating" in about 40% of located nests), final clutch size, hatching success (percentage of eggs hatched), and fledging success (percentage of hatched eggs producing fledged young). Fledging success was estimated by inspection of nests just before and after fledging. Three nests (2 Pygmy Nuthatch and 1 Western Bluebird) were detected in natural cavities on the Thinned treatment plot but were not inspected because of inaccessibility. All other nests on the Open and Thinned treatment plots were in nest boxes.

I estimated breeding densities using the spot-map method and made 8-10 census visits/breeding season to each plot. I supplemented these visits by searching for nests in natural cavities. Density estimates presented here are expressed as number of breeding pairs/40 ha.

I analyzed the relationship between breeding density and reproductive output on the treatment plots with analyses of covariance (ANCOVA) and tested the null hypotheses that variation in nest success, clutch size, hatching success, and fledging success were not related to breeding density. I used a repeated-measures design with plot and species as the grouping variables and density as the covariate. This design enabled evaluation of the additive effects of breeding density on reproductive output over and above those attributable to species, plot, and year. Repeated-measures analyses were necessary because treatments were not randomized with respect to plots across years (for details of the design structure used here, see Dixon 1983: 359-412). For the hypotheses considered here, nests of a given species, on a plot, within a breeding season could not be considered independent observations, and I used averaged values as response variables. The reproductive output of Western Bluebirds on the Thinned treatment plot and Control plot was compared using t-tests with Bonferroni adjustment of alpha probability.

I found 110 nests in boxes from 1981 through 1983. Western Bluebirds were the most common box occupant ($n = 51$), Pygmy Nuthatches were the least ($n = 24$), and Violet-green Swallows were intermediate ($n = 35$). Overall sample size was greater on the Thinned treatment plot ($n = 61$). I also located 8 bluebird nests in natural cavities on the Control plot.

Densities on the treatment plots generally increased between each successive breeding season (Table 1) because of increasing frequency of box occupancy (Brawn et al. 1987). Exceptions to this trend were swallows on the Open and nuthatches on the Thinned treatment plots between 1982 and 1983. Variation in breeding densities among years ranged from 20% for swallows on the Open treatment to over 300% for swallows on the Thinned treatment plot. Bluebird densities on the Control plot were relatively stable and 33-50% of the densities found on the Thinned treatment plot.

Overall, 86% ($n = 95$) of the nests found in boxes resulted in at least 1 fledged young. All bluebird nests on the Control plot were successful (Table 1). Nest success on the Thinned treatment plot (89%) was higher than that on the Open plot (81%). Overall nest success was 74% for Violet-green Swallows, 88% for Pygmy Nuthatches, and 92% for Western Bluebirds. The primary cause of nest failure was predation during the nestling period ($n = 7$). The known or suspected predators were grey-necked chipmunks (*Eutamias cinereicollis*). Chipmunk activity could have been an expression of competition for nest sites as they also nested in boxes (Brawn 1985).

The frequency of nest failure was unrelated to breeding density (ANCOVA regression coefficient = 0.001, $F_{1,1} = 0.01$, $P = 0.99$). No systematic relationship between nest failure and breeding density was apparent within any species (Table 1). For example, in 1982 on the Open treatment plot, Violet-green Swallow nest success was relatively low but increased the following year when their densities decreased. On the Thinned treatment plot, I observed the opposite trend in 1982 and 1983. Bluebird nest success was the same on the Thinned treatment and Control plots in 1982 and 1983 despite large differences in breeding densities.

Clutch sizes found in boxes varied among species, years, and plots (Table 1) but were independent of breeding density (ANCOVA regression coefficient = 0.042, $F_{1,1} = 1.66$, $P = 0.42$). Bluebird clutch sizes were not significantly different on the Thinned treatment and Control plots (t-tests with Bonferroni adjustment of probability, $P > 0.60$). The date of clutch initiation can confound density effects if nesting phenology is variable because late clutches are often relatively small (Järvinen and Lindén 1980, Alatalo and Lundberg 1984). I found the date of clutch initiation to be highly variable between plots and among years (Brawn pers. obs.); however, density effects remained insignificant when this variation was accounted for by including the date of clutch initiation as a second covariate (ANCOVA regression coefficient = 0.071, $F_{1,1} = 1.86$, $P = 0.36$). This adjustment refuted certain apparent positive density effects on clutch size. For example, the average clutch size and breeding density of swallows increased on the thinned-habitat treatment plot between 1981 and 1982; however, the average date of clutch initiation was about 2 weeks earlier in 1982. I observed similar increases in bluebirds, but, in contrast to swallows, the year with larger clutches averaged 8 days later than the previous year. Thus, I found no consistent relationship between clutch size and breeding phenology. Average dates of bluebird clutch initiation on the Thinned treatment and Control plots were nearly identical.

The proportion of eggs hatching on the treatment plots (Table 1) was not significantly influenced by breeding density (ANCOVA regression coefficient = 0.004, $F_{1,1} = 0.02$, $P = 0.93$), and bluebird hatching success was not significantly different on the Thinned treatment and Control plots (t-tests with Bonferroni adjustment of probability, $P > 0.75$). Hatching success also varied according to plot and year and was highly variable among species. Violet-green Swallows had lower overall hatching success (78%) than either nuthatches (84%) or bluebirds (90%). Egg infertility (determined by field inspection) was the most frequent cause of hatching failure (65% of unhatched eggs), followed by absence of parents (18%).

The pattern of variation in fledging success was consistent with the other measures of reproductive output. I found plot, year, and interspecific variation (Table 1) but no evidence of density effects (ANCOVA regression coefficient = −0.005, $F_{1,1} = 0.05$, $P = 0.87$). The overall fledging success of each species was nearly identical to their hatching success. Western Bluebird fledging success was similar on the Thinned treatment and Control plots (t-tests with Bonferroni adjustment of probability, $P > 0.85$).

These results, though consistent, should be interpreted with caution. Sample sizes were relatively small for each species in certain years. In addition, my results are potentially confounded by the age (i.e. breeding experience) of birds breeding on the treatment plots. Rapid density increases subsequent to provision of nest boxes can result in a locally high proportion of first-year breeders (Eriksson 1982).

TABLE 1. Breeding densities and reproductive output of cavity nesters in northern Arizona.

		Violet-green Swallow		Pygmy Nuthatch		Western Bluebird		
Variable		Open treatment	Thinned treatment	Open treatment	Thinned treatment	Open treatment	Thinned treatment	Control
Density	1981	—	12.5	8.7	22.5	23.9	27.5	—
(pairs/40 ha)	1982	22.0	45.0	12.0	30.0	40.0	37.0	20.0
	1983	17.5	50.0	17.5	25.0	65.0	50.0	16.3
% nest success	1981	—	100 (4)	100 (2)	100 (5)	75 (8)	83 (6)	—
(n)	1982	20 (5)	56 (9)	100 (2)	100 (5)	89 (9)	100 (7)	100 (4)
	1983	100 (3)	93 (14)	67 (6)	75 (4)	100 (14)	100 (7)	100 (4)
Clutch size[a]	1981	—	3.3 (0.96, 4)	8.5 (0.70, 2)	8.0 (1.9, 5)	5.5 (0.53, 8)	4.3 (1.6, 6)	—
	1982	3.2 (0.84, 5)	4.1 (0.78, 9)	7.5 (0.70, 2)	7.6 (0.55, 5)	5.5 (0.44, 9)	5.1 (0.69, 7)	5.3 (0.54, 4)
	1983	3.3 (1.5, 3)	4.3 (0.73, 14)	7.7 (0.82, 6)	7.5 (1.3, 4)	5.2 (0.43, 14)	5.0 (0.58, 7)	5.0 (0.61, 4)
% hatching	1981	—	77 (88, 4)	82 (50, 2)	90 (18, 5)	82 (50, 8)	85 (44, 6)	—
success[a]	1982	70 (73, 5)	78 (98, 9)	100 (0, 2)	85 (61, 5)	94 (29, 9)	83 (18, 6)	85 (19, 4)
	1983	70 (55, 3)	81 (109, 14)	83 (135, 6)	70 (29, 4)	97 (48, 14)	94 (39, 7)	86 (12, 4)
% fledging	1981	—	100 (0, 4)	100 (0, 2)	91 (29, 4)	86 (14, 6)	100 (0, 6)	—
success[a]	1982	36 (124, 5)	59 (61, 9)	100 (0, 2)	92 (42, 4)	77 (24, 8)	87 (25, 6)	82 (16, 4)
	1983	86 (64, 3)	91 (41, 14)	61 (53, 6)	76 (37, 3)	92 (33, 14)	100 (0, 7)	100 (0, 4)

[a] $\bar{x}$ (SD, n).

Without provision of nest boxes, these young birds (especially males) probably would not breed because of a shortage of nest sites (von Haartman 1971, Belman 1980). Breeding-site tenacity is often pronounced in secondary cavity nesters (von Haartman 1971), and the proportion of first-year birds probably decreases after abrupt initial density increases. Increasing age of breeding birds on my plots could have offset potentially negative density effects because reproductive success typically increases with experience (Perrins 1979).

I had adequate information on the ages of male Western Bluebirds only. From observation of males banded as nestlings and plumage (blue on first-year males appears dull), I estimate that from 1981 through 1983, the proportion of second-year or older breeding males increased from 33% to 42% on the dense habitat and from 25% to 50% on the open habitat. Reproductive success of breeding pairs that included experienced males was slightly higher ($\bar{x}$ fledging success approx. 5% greater) than those with known or suspected first-year males; however, age effects on bluebird breeding success were minor compared with year and plot effects (Brawn in prep.). Orell and Ojanen (1983) reported similar findings with box-nesting Great Tits in northern Finland.

The once-vehement debate over the relative influence of density-dependent vs. density-independent effects (see Murray 1979) has been tempered by a realization that such an "either/or" dichotomy is illusory (Milne 1957, Ito 1961, Strong 1986). Studies on noncolonial passerines advance no consensus because density effects can be negative (Dhondt 1977, Goosen and Sealy 1982), absent or intermittent (Tompa 1967, Järvinen 1980, Alatalo and Lundberg 1984), or even positive (Robertson and Norman 1977).

When detected, negative density effects are often attributed to predators such as weasels (*Mustela nivalis*; Dunn 1977) or intraspecific competition for food (Lack 1966). Cavity-nest predators with effects equivalent to weasels were apparently rare on my study plots. I observed that food can indeed influence the reproductive success of birds in northern Arizona (Brawn in prep.). I found no relation, however, between the intensity of this influence and breeding density or presumed strength of intraspecific competition, a result consistent with other studies conducted in northern (i.e. high latitude or altitude) environments (Järvinen 1980, 1983; Orell and Ojanen 1983; Virolainen 1984).

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Metabolic Rate and Thermostability in Relation to Availability of Yolk in Hatchlings of Black-legged Kittiwake and Domestic Chicken

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Hatchlings, especially in precocial species, have a relatively large amount of yolk that can be used up to 6 days after hatching if growth, thermoregulatory, and locomotive costs are minimal (Pettit et al. 1985). Marcström (1960, 1966) showed by carcass analyses that yolk is used for both catabolism and synthetic purposes in the Common Capercaillie (*Tetrao urogallus*) and the Mallard (*Anas platyrhynchos*). In Canada Geese (*Branta canadensis*) newly hatched goslings will grow in spite of being starved (Peach and Thomas 1986). If, as suggested by these studies, the yolk reserve is used not only for catabolism but also for synthetic purposes, the result would produce a higher metabolic rate not reflecting a true basal metabolic rate (BMR).

We attempted to estimate the possible difference in metabolic rate in chicks with and without a yolk reserve. The yolk sacs of newly hatched chicks of the Black-legged Kittiwake (*Rissa tridactyla*) and domestic chicken (*Gallus gallus*) were removed surgically. The metabolic rate in these chicks was compared with that measured in sham- and nonoperated chicks.

Hatching eggs of kittiwakes were collected in Kongsfjorden, Spitsbergen, and taken to the laboratory of the Norwegian Polar Research Institute in Ny Ålesund. The eggs were hatched in a commercial incubator, and the chicks were used in experiments 3-6 h after hatching. Newly hatched chickens were obtained from a commercial farm and used in the experiments at the Department of Zoology of the University of Trondheim approximately 2 days after hatching. The hatchlings received only water and were kept under thermoneutral conditions.

Chicks of both species were divided randomly into three groups: operated, sham-operated, and nonoperated. Sham- and nonoperated chicks formed the control group. The chicks of the operated and the sham groups were anesthetized with ether; lidocaine was used as a local anaesthesia. In both groups the abdominal cavity was opened. In the operated group the yolk sac was removed and weighed. The chicks recovered within 30 min, and oxygen consumption was measured approximately 3 h later.

Before measurement of oxygen consumption the chicks were weighed, and, in the case of the kittiwakes, a copper-constantan thermocouple was inserted into the rectum. Oxygen consumption in kittiwakes was measured using a manometric respirometer (Bech et al. 1984). In the chickens oxygen consumption was measured using an open-flow system in which the air was sucked through a 0.9- or 2.4-l metabolic chamber with a flow rate of 1 l/min. After drying over silica