ROSENFIELD, R. N., AND J. BIELEFELDT. 1993. Cooper's Hawk (*Accipiter cooperii*). *In* A. Poole and F. Gill [eds.], The birds of North America, No. 75. The Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, DC.

ROSENFIELD, R. N., AND D. L. EVANS. 1980. Migration incidence and sequence of age and sex classes of the Sharp-shinned Hawk. Loon 52:66–69.

SMALLWOOD, J. A. 1988. A mechanism of sexual segregation by habitat in American Kestrels (*Falco sparverius*) wintering in south-central Florida. Auk 105:36–46.

SNYDER, N. F. R., AND J. W. WILEY. 1976. Sexual size dimorphism in hawks and owls of North America. Ornithol. Monogr. 20.

SPSS, INC. 1997. SYSTAT® 7.0: new statistics. SPSS, Inc., Chicago.

WOODREY, M. S., AND C. R. CHANDLER. 1997. Age-related timing of migration: geographic and interspecific patterns. Wilson Bull. 109:52–67.

The Condor 101:678–681

FACULTATIVE COMMUNAL BROOD REARING IN CALIFORNIA QUAIL[1]

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Abstract. We examined communal brooding in California Quail *Callipepla californica.* Most broods are reared by their parents alone, but 23 of 195 (12%) broods combined and were reared communally by all their living parents. A 26% greater fledgling rate of communally reared chicks was not statistically significant. Parents of communal broods lived significantly longer (3.1 years) than parents of single broods (1.9 years) and hatched significantly more young (36.3 vs. 15.7 young) during their lifetimes. Those that raised their first surviving brood communally were significantly (2.8 times) more likely to hatch a brood the following year. Communal brood fathers sentineled significantly less and ate significantly more. We do not know whether parents initiated brood merging, thereby increasing their direct fitness, or the young initiated brood merging, thereby increasing their inclusive fitness. Broods combined only when they were hatched from nearby nests. Communal brood rearing may be constrained by the absence of pre-hatch contact between the parents, or by the limited mobility of young chicks.

Key words: California Quail, Callipepla californica, *communal broods, fitness.*

Both cooperative parental care and nuclear family care occur in several species of birds. Most are altricial species nesting in a single nest (e.g., Stacey and Koenig 1990, Armstrong and Juritz 1996). California Quail (*Callipepla californica*) are not known to nest together, but we and J. Calkins (pers. comm.) have observed broods merging posthatch and being reared together. Brown et al. (1998) report merged broods in Gambel's Quail (*Callipepla gambelii*).

Cooperative care in Acorn Woodpeckers (*Melanerpes formicivorus*) (Koenig and Mumme 1987) and Groove-billed Ani (*Crotophaga sulcirostris*) (Koford et al. 1990) increases the parents' longevity, but decreases the annual per adult production of fledglings. Posthatch aggregation of precocial young occurs in Common Eiders (*Somateria mollissima*), and in some predation regimens such aggregation contributes to increased duckling survival (Mendenhall 1975, 1979, Munro and Bedford 1977). Munro and Bedford (1977) speculate that mothers that combine broods also may benefit via longer reproductive lives. Cooperating California Quail parents provide an opportunity to examine whether the benefit of increased longevity can be realized without paying the cost of decreased per capita fledgling production.

When the young cannot initiate brood merging, the analysis of inclusive fitness benefits focuses on the generations that preceded the nestlings—the parents and older siblings. But precocial young initiate brood merging in some species. Deserted Barrow's Goldeneye ducklings (*Bucephala islandica*) join other broods, and benefit from the joined broods' maternal protection (Eadie and Lyon 1998). Canada Goose (*Branta canadensis*) goslings are sometimes reared in "gang broods" formed when the goslings of one set of parents join the goslings of another set (Sherwood 1967, Nastase 1983), and combined nuclear families including both sets of parents formed by goslings from two broods joining together have been observed (J. Eadie, pers. comm.; D. Lott, pers. observ.). The fitness consequences of those combined broods are not known, but if they increase the parent's lifetime reproductive success, the young are raising their own inclusive fit-

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ness. Our goals are to describe communal brood rearing behavior in California Quail and assess its potential direct and indirect fitness benefits.

METHODS

California Quail are relatively small (160 g) granivorous/herbivorous galliformes. Plumage is dimorphic and males are slightly larger than females. Their native range extends over most of California and Baja California, Mexico below 1,500 m. Their natural annual mortality is about 70% year^{-1} (Emlen 1940, Raitt and Genelly 1964). In late summer, mated pairs and their adult-sized young coalesce into coveys (Johnsgard 1973, Leopold 1977) that roost and forage as units (Sumner 1935, Howard and Emlen 1942). Dispersal begins in the fall and continues into the beginning of the breeding season. Most yearling males disperse to a nearby area (Emlen 1939, Raitt and Genelly 1964). Young females rarely disperse except as members of a pair (Emlen 1939, Howard and Emlen 1942). In virtually all populations, female mortality is higher, so there are usually more males (Emlen 1940). In February or March, males begin to compete for access to, and defend, females within the covey. From March through June, the mated males' aggression keeps the pairs temporally isolated in their extensively overlapping home ranges (Sumner 1935, Raitt 1960).

The female incubates continuously except for short feeding breaks. The male perches nearby while she incubates, preventing unmated males from approaching her, and probably serving as a sentinel against predators. Both parents accompany the highly precocial young. The male spends most of his time acting as a sentinel with no opportunity to feed. Parents are usually aggressive toward other families, attacking both parents and young chicks (Howard and Emlen 1942).

We observed free ranging California Quail at the University of California Sierra Foothills Field Station, 18 km northeast of Marysville, California. Our subjects occupied a well defined drainage of 140 ha of brushy grassland grazed by cattle. This drainage was not hunted during those years, but was hunted prior to them, and individuals from nearby hunted areas immigrated during our study. During our study years (1983 through 1988), the mean number of individuals was 112 (range 61–159). We observed the quail from a 5-m tower at the foot of the drainage bowl and other vantage points using 10× binoculars and a 20–60× spotting scope. The distance from observer to subject ranged from 1–300 m, and the modal distance was about 100 m.

During November, December, and January of each study year, we trapped as many individuals as we could in funnel traps baited with seed. Each trapped individual was marked with a unique combination of colored leg bands and classified as young of the year or adult by its plumage (Leopold 1977). Because the observation tower was placed at the bottom of the drainage bowl and the area was grazed, observers could read leg bands and identify individuals. We searched adjoining areas but, like Emlen (1939), never located a bird that had mated and nested in our area. Therefore, when an adult disappeared we assumed it had died. Sixty-six of those banded as young of the year hatched young and apparently died before the end of our study Twelve apparently died without hatching young. This allowed us to determine each bird's lifetime reproductive output, and to compare the output of communal and non-communal parents.

Of all the birds we banded (n = 158), 102 remained in our study area. At the end of the study, 24 of these were still alive and thus not included in our results. If these 24 were still alive because they were exceptionally long-lived, our study sample would have been biased against long-lived individuals. Of these 24, the number of survivors per age group was: 15 months = 17 (9 males, 8 females), 27 months = 4 (2 males, 2 females), 39 months = 2 (1 male, 1 female), and 51 months = 1 female. Because most of the survivors were quite young, we conclude that few were still alive because they were exceptionally long-lived.

The observer divided each day's observation hours into 15 min blocks. He started searching for a specific individual at the start of the block. When he found that individual during the block, he recorded its behavior during the remaining time. The observer worked through a list of all animals recently alive in a fixed order, starting each day with the individual that followed the previous day's last individual. This distributed repeated observations on each individual over the daylight hours, assuring that sampling of each individual recorded for several hundred minutes represented the entire day.

We recorded behavioral interactions and reproductive outcomes by dictating the observations into a tape recorder and later transcribing them for analysis. We sampled behavioral events via focal animal sampling, and sampled states on an all events basis (Altmann 1974). Communal broods were defined as the chicks from more than one nest combined, with at least one parent of each nuclear brood accompanying the combined brood. Values are reported as means ± SD. For inferential statistical tests we used Minitab software (Ryan and Joiner 1994).

RESULTS

In all, 23 of 195 broods (12%) were combined with one or more other broods, creating 11 communal broods from 1983 through 1988. One communal brood was very large, consisting of seven adults (four males and three females) and 41 chicks. Two communal groups were formed when each of two widowed females combined her brood with a pair's brood. We saw each nuclear brood after it hatched and before it became part of a communal brood. All communal broods were formed of broods from neighboring nests. We have precise data on the distance between nine of the pairs of nests from which communal broods formed. This distance (10.7 ± 4.0 m) was less than the distance between the next most proximate 18 pairs of nests, none of which formed communal broods (97.7 ± 47.8 m) (Mann-Whitney test, $W = 45$, $P < 0.001$). Eleven communal broods were observed from 1983 through 1988.

We documented chick survival to 14 weeks in 6 communal broods and 17 non-communal broods reared in 1987 and 1988. In communal broods, 77%

survived, whereas in non-communal broods 61% survived. This difference is not statistically significant (Fisher exact test, $P = 0.30$).

Ten adults that participated in communal broods at least once disappeared and almost certainly died before the end of our study, as did 56 adults that participated only in non-communal broods. The 10 communal parents lived significantly longer: 3.1 ± 1.0 vs. 1.9 ± 0.8 years (Mann-Whitney, $W = 1695$, $P < .001$). Communal parents hatched more chicks: 36.3 ± 11.7 vs. 15.7 ± 8.6 (independent $t_{64} = 5.30$, $P < .001$) in more breeding seasons: 2.3 ± 0.7 vs. 1.5 ± 0.7 (Mann-Whitney, $W = 1724.5$, $P < 0.01$).

Eight adults raised their first surviving brood communally; of these, seven (87.5%) also hatched a brood the following year. Fifty-eight raised their first surviving brood as a nuclear family; of these, only 18 (31%) also hatched a brood the following year. This difference is highly significant (Fisher exact test, $P = 0.004$). Thus, the longer lives and increased lifetime reproduction of communal parents was apparently related to participation in communal brood rearing early in their reproductive career.

One reason for increased longevity is suggested by comparing the time budgets of five communal brood males and nine non-communal brood males which we had observed for more than 15 hr each. Each male's data was summarized as a single data point in each of three categories: percent time (1) vigilant, (2) feeding, and (3) resting. The communal brood males spent less time vigilant (42.6 ± 4.8% vs. 73.0 ± 5.7%) and more time feeding (36.2 ± 5.5% vs. 14.5 ± 2.6%) and resting (21.2 ± 4.2% vs. 13.4 ± 4.2%). All these differences are statistically significant (independent t_{12}, two-tailed $P < 0.01$).

DISCUSSION

Twelve percent of California Quail broods were raised communally. Parents that raised their first surviving brood communally lived longer and hatched more young. The correlation of communal brooding in California Quail with greater longevity and more broods does not by itself demonstrate causality. If there were a fixed probability of rearing a brood communally in any given year, adults that lived longer would be more likely to have raised a brood communally. But if communal brood rearing did not affect longevity, communal rearing would be as likely to follow single family brood rearing as to precede it. In fact, parents that reared their first surviving brood communally were more likely to hatch additional broods. This supports the notion that communal brood rearing extends an individual's reproductive career.

Communal nesting and brood rearing also was related to increased longevity of parental Groove-billed Anis (Koford et al. 1990) and Acorn Woodpeckers (Koenig and Mumme 1987), but in these altricial species communal groups fledged fewer young adult^{-1} year^{-1}. Pukeko (*Porphyrio porphyrio*) young are precocial with respect to locomotion, although they must be fed for several weeks. Communal groups nest in a single nest and, again, per capita production decreases as group size increases (Craig and Jamieson 1990). There was no evidence of such a trade-off in California Quail. Combining broods posthatching avoids prehatch costs such as egg destruction or inadequate incubation of a large combined clutch.

We do not know whether the parents or the chicks initiate brood merging. The parents would increase their lifetime reproductive success by initiating brood merging. If the quail chicks initiate brood merging, they would increase their inclusive fitness by extending their parents' reproductive careers giving each chick more siblings at no cost to themselves. Because the fitness gain must be assigned to those that initiate brood merging, it will be important to identify the initiators.

The greater survival of communal males may be due in part to their increased foraging compared to non-communal males, which is likely to reduce the weight loss typical of brood-rearing males (Sumner 1935, Riatt 1960). We have not identified a mechanism to increase female survival, but both sexes may benefit from reduced predation via dilution (Calvert et al. 1979) or increased predator detection (Kenward 1978).

Given its advantages, it is somewhat surprising that communal brood rearing is not more frequent. Because only neighboring broods merge, merging may depend on adults developing mutual tolerance of their neighbors during mating and incubation, and/or be constrained by the limited mobility and small home range of young chicks. Because females seldom disperse, merged broods might be related through their mothers.

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LITERATURE CITED

ALTMAN, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

ARMSTRONG, A. J., AND J. JURITZ. 1996. Prediction of cooperative breeding by terrestrial bird species in South Africa. Ostrich 67:1–8.

BROWN, D. E., J. C. HAGELIN, M. TAYLOR, AND J. GALLOWAY. 1998. Gambel's Quail (*Callipepla gambelii*). *In* A. Poole and F. Gill [eds.], The birds of North America, No. 321. The Birds of North America, Inc., Philadelphia.

CALVERT, W. H., L. E. HEDRICK, AND L. P. BROWER. 1979. Mortality of the monarch butterfly, *Danaus plexippus*: avian predation at five over-wintering sites in Mexico. Science 182:1272–1275.

CRAIG, J. L., AND I. G. JAMIESON. 1990. Pukeko: different approaches and some different answers, p. 387–414. *In* P. B. Stacey and W. D. Koenig [eds.], Cooperative breeding in birds. Cambridge Univ. Press, Cambridge.

EADIE, J. MCA., AND B. E. LYON. 1998. Cooperation, conflict and creching behavior in Goldeneye Ducks. Am. Nat. 151:397–408.

EMLEN, J. T., JR. 1939. Seasonal movements of a low-

density Valley Quail population. J. Wildl. Manage. 3:118–130.
EMLEN, J. T., JR. 1940. Sex and age ratios in survival of the California Quail. J. Wildl. Manage. 4:92–99.
HOWARD, W. E., AND J. T. EMLEN JR. 1942. Intercovey social relationships in the Valley Quail. Wilson Bull. 54:162–170.
JOHNSGARD, P. A. 1973. Grouse and quails of North America. Univ. Nebraska Press, Lincoln, NE.
KENWARD, R. E. 1978. Hawks and doves: factors affecting success and selection in goshawk attacks on wood-pigeons. J. Anim. Ecol. 47:449–460.
KOENIG, W. D., AND R. L. MUMME. 1987. Population ecology of the cooperatively breeding Acorn Woodpecker. Princeton Univ. Press, Princeton, NJ.
KOFORD, R. R., B. S. BOWEN, AND S. L. VEHRENCAMP. 1990. Groove-billed Anis: joint-nesting in a tropical cuckoo, p. 333–355. *In* P. B. Stacey and W. D. Koenig [eds.], Cooperative breeding in birds. Cambridge Univ. Press, Cambridge.
LEOPOLD, A. S. 1977. The California Quail. Univ. California Press, Berkeley, CA.
MENDENHALL, V. M. 1975. Growth and mortality factors of Eider ducklings (*Somateria m. mollissima*) in north-east Scotland. Ph.D. diss., Univ. Aberdeen, Aberdeen, Scotland.
MENDENHALL, V. M. 1979. Brooding of young ducklings by female Eiders *Somateria mollissima*. Ornis Scand. 10:94–99.
MUNRO, J., AND J. BEDARD. 1977. Gull predation and creching behaviour in the Common Eider. J. Anim. Ecol. 46:799–810.
NASTASE, A. J. 1983. Behavioral ecology of the Canada Goose *Branta canadensis canadensis*. Ph.D. diss., Univ. Pittsburgh, Pittsburgh, PA.
RIATT, R. J., JR. 1960. Breeding behavior in a population of California Quail. Condor 62:284–292.
RAITT, R. J., AND R. D. GENELLY. 1964. Dynamics of a population of California Quail. J. Wildl. Manage. 28:127–141.
RYAN, B. E., AND B. L. JOINER. 1994. Minitab handbook. 3rd ed. Duxbury Press, Belmont, CA.
SHERWOOD, G. A. 1967. Behavior of family groups of Canada Geese, p 340–355. *In* Trans. 32nd N. Am. Wildl. Nat. Resource Conf., Wildl. Manage. Inst., Washington, DC.
STACY, P. B., AND W. D. KOENIG. 1990. Cooperative breeding in birds: long term studies of ecology and behavior. Cambridge Univ. Press, Cambridge.
SUMNER, E. L., JR. 1935. A life history study of the California Quail, with recommendations for its conservation and management. Calif. Fish Game 21:167–253, 275–342.

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INCUBATION BEHAVIOR OF LONG-TAILED TITS: WHY DO MALES PROVISION INCUBATING FEMALES?[1]

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Abstract. The incubation period of Long-tailed Tits *Aegithalos caudatus* is highly variable, ranging from 14 to 21 days. Females alone incubate the eggs, but males provide females with some food during the incubation period, although females must also forage for themselves. Our aim was to investigate whether male provisioning of incubating females influenced female incubation behavior and the length of the incubation period. Provisioning rates varied between males, and female nest attentiveness was negatively related to short-term variation in the rate at which their partner fed them. However, the provisioning rate of individual males also varied significantly through time, and there was no significant effect of male care on female incubation across the whole incubation period. There was no evidence that variation in the behavior of either males or females influenced the length of the incubation period.

Key words: Aegithalos caudatus, *courtship feeding, incubation, Long-tailed Tit.*

Male birds often provide food for females during the breeding season, behavior known as courtship feeding. Provisioning may occur during pairing or egg-laying, but it also is frequent during the incubation period (Ricklefs 1974). The traditional interpretation of courtship feeding is that it serves a pair-bonding function, helping to cement the relationship between breeding partners (Lack 1940, Kluijver 1950). A second hypothesis proposes that courtship feeding provides information to females about male quality, in particular, his ability to feed nestlings (Nisbet 1973, 1977). Female fitness may depend on the extent of paternal care (Lyon et al. 1987, Yasukawa et al. 1990, Davies and Hatchwell 1992), so such information, and male ad-

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