Post-hatching brood amalgamation in Northern Bobwhites

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ABSTRACT. Our understanding of the frequency of brood amalgamation in the Northern Bobwhite (*Colinus virginianus*) is largely anecdotal. Information on it is important in understanding survival and reproduction. We captured entire bobwhite broods at 3–4 and 10–12 d of age and individually marked each bobwhite chick within a brood. Broods were considered amalgamated if novel unmarked or marked individuals or significant differences in body mass or flight ability among chicks were observed. During 2002, minimum frequencies of brood amalgamation within bobwhite broods were 6.7% at 3–4 d and 20.7% for 10–12 d-old broods. During 2003, minimum frequencies of brood amalgamation ranged from 0.0% at 3–4 to 22.2% for 10–12 d-old broods. Our results indicate bobwhites exhibit higher rates and earlier onset of brood amalgamation than previously documented among the Galliformes. Causes of brood amalgamation in bobwhite may differ from those proposed for waterfowl due to the bobwhite's limited mobility, short lifespan, gregarious behavior, and resulting potential for relatedness among individuals. Molecular techniques should be used to assess the effects of inclusive fitness losses and gains among bobwhites that donate and receive chicks. Bobwhite researchers should recognize the potential bias in chick survival estimates caused by high rates of brood amalgamation.

SINOPSIS. **Mezcla polluelos parvadas de *Colinus virginianus***
La frecuencia en que se mezclan o amalgaman parvadas de polluelos de la codorniz (*Colinus virginianus*), es anecdótica. Capturamos parvadas completas de polluelos de 3–4 y de 10–12 días de edad y marcamos a cada individuo dentro de la parvada. Las parvadas se consideraban amalgamadas, si se observaban individuos nuevos sin marcar con individuos marcados y/o se encontraban diferencias significativas en la masa corporal o habilidad para volar entre los polluelos. Durante el 2003 la frecuencia mínima de mezcla entre parvadas de codornices fue de 6.7% a la edad de 3–4 días y 20.7% entre los 10–12 días. Nuestros resultados indican que las codornices muestran una taza mayor y a más temprana edad que lo previamente documentado para Galliformes. Las causas de estas mezclas en estas aves pudieran ser diferentes a las propuestas para aves acuáticas, dada la capacidad limitada de movimiento de las codornices, corta longevidad y conducta de agregarse lo que da lugar a un potencial mayor de relacionarse los individuos. Se deben utilizar técnicas moleculares para determinar la ganancia o perdida en adaptabilidad (en términos de supervivencia) entre parvadas que ganan o pierden individuos. Los que estudian a estas codornices deben reconocer el sesgo potencial en los estimados de supervivencia dada la alta tasa de mezcla que puede haber en los grupos.

Key words: brood mixing, chick capture, chick marking, Northern Bobwhite, post-hatching brood amalgamation

Except in water fowl, brood amalgamation is relatively unstudied in birds with precocial young. Post-hatching brood amalgamation (hereafter brood amalgamation) occurs when organisms incubate and hatch their own young then group their offspring with those of other individuals. Brood amalgamation may be grouped into four categories defined by Eadie et al. (1988) and Afton and Paulus (1993): (1) adoption, foster young are accepted into the broods of single or paired individuals, (2) creching, two or more unrelated offspring are cared for by groups of birds containing several adults, which may or may not be related to the young, (3) gang-brooding, pairs or single adults group their respective broods together, and (4) kidnapping, young are forcibly removed from the broods of sub-dominant pairs/individuals for recruitment into the broods of dominant pairs/individuals.

Beauchamp (1997) reported 38% of waterfowl species examined ($N = 162$) were found to exhibit varying degrees of brood amalgamation; however, the frequency of mixing within species was not reported. Frequencies of mixing as high as 28% ($N = 25$) have been reported among broods of Canada Geese (*Branta canadensis*; Nastase and Sherry 1997). One or more kinds of brood amalgamation have also been

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reported among Ostriches (*Struthio camelus*) and in some galliforms (Erwin, in Leopold 1977; Bertram 1992; Brown et al. 1998; Lott and Mastrup 1999). Among Galliformes, neither the occurrence nor the frequency of brood amalgamation has been well documented, and data suggesting its occurrence are largely anecdotal. Adoptions of chicks by Ruffed Grouse (*Bonasa umbellus*) have been noted on several occasions (Chambers and Sharp 1958; Maxson 1978). Erwin (in Leopold 1977) reported the occurrence of brood amalgamation among California Quail (*Callipepla californica*) based on observation of nine broods containing ≥20 chicks, and Lott and Mastrup (1999) reported a 12% frequency of brood amalgamation ($N = 195$) for the same species. The occurrence of brood amalgamation, in both cases, was based on size and plumage dimorphism among members of broods and the number of individual offspring in broods. Gambel's Quail (*C. gambelii*) have also been reported to exhibit brood amalgamation (Brown et al. 1998).

Stoddard (1931) first discussed the potential for brood amalgamation among Northern Bobwhites after conducting a series of adoption trials using penned birds. He found 90% of individuals adopted unrelated chicks placed in their pens. Based on capture records collected during fall, Stoddard (1931) theorized that amalgamation of broods was occurring among wild birds. Lehmann (1984) reported lone females with young were likely to join other females with similarly-aged young, and he noted that several bobwhite families were observed with extra adults or young. Three percent of bobwhite broods in Oklahoma exhibited a net gain of chicks from hatching to 20 d old, and 25.4% of broods exhibited net gains from hatching to 29–30 d old (DeMaso et al. 1997). Anecdotal reports of brood mixing among bobwhites in Missouri were also presented by Burger et al. (1995).

Few studies have tracked broods of individually marked, immature Northern Bobwhites through the early life stages (1–12 d). Given the nature of contemporary population and survival estimation techniques, objective estimates of brood amalgamation rates are particularly important (Flint et al. 1995; DeMaso et al. 1997). Studies are typically limited in their ability to radio-locate immature bobwhite due to limitations imposed by transmitter size and

battery-life. Typically, only adult bobwhites are radio-tagged. Therefore, chick survival estimates are acquired from summer flush-counts of bevies associated with radio-tagged adults or modeling approaches based on fall/winter recruitment estimates (DeVos and Mueller 1993; Burger et al. 1995; DeMaso et al. 1997; Mueller et al. 1999). Without taking into account such factors as brood amalgamation, these methods can lead to inflated estimates of immature bobwhite mortality, inaccurate population growth predictions, and spurious conclusions regarding causes and patterns of mortality (Flint et al. 1995). Additionally, brood amalgamation has potentially important consequences for formation of social groups (coveys) during the non-breeding season in bobwhites and other galliforms (Stoddard 1931; Jenkins 1961).

In this study, we followed individually marked Northern Bobwhite chicks throughout the early life stages to determine the degree of brood amalgamation. We discuss prevailing theory and application of this research to the ecology of galliforms, and we address several hypotheses to explain the occurrence of brood amalgamation among Northern Bobwhites.

METHODS

We captured adult and subadult bobwhites during October–June 2002 and 2003 on a 300-ha area of Tall Timbers Research Station, Tallahassee, Florida, using funnel traps (Stoddard 1931) baited with grain sorghum. We located approximately 15 coveys based on intensive pointing-dog searches of the study area and radio-locations of previously captured birds. Traps were placed throughout the study area so that ≥5 traps were within the estimated home range of each covey. We attempted to mark approximately 70% of individuals in each covey. Weight, sex, and age (subadult or adult) of birds caught in traps were determined following capture. Aluminum leg bands with unique number combinations were applied to all birds captured. Birds >150 g were fitted with a 6-g necklace-style radio-transmitter (American Wildlife Enterprises, Monticello, Florida).

During the breeding season (April–October), we located birds by radio-telemetry at least once per day, and individuals found in the same location for >1 d were assumed to be nesting.

Areas in which suspected nests were identified were flagged on all sides >3 m from the estimated nest location. We searched these areas for the presence of a nest and for an egg count when a radio-location indicated the bird was away from its nest. Upon successfully hatching, broods with a radio-tagged adult were located at least once per day.

Brood capture and marking. Brood capture procedures followed Smith (2002) and Smith et al. (2003). Adult birds and their broods were located by radio-telemetry 2 h prior to sunrise on the day of capture. While roosting, the adult(s) and brood were surrounded by a circular enclosure composed of 6–8 individual panels (3 m wide × 0.75 m high) placed approximately 1.5 m from the center of the brood's location. All edges of the enclosure were buried to prevent escape of chicks. At sunrise, all vegetation surrounding the brood within the enclosure was removed until the adult(s) flushed from the roost site. Chicks were collected from within the enclosure until all had been captured.

During May–October 2002 and 2003, two captures were conducted for broods at 3–4 and 10–12 d after hatching to minimize marking-related effects on immature individuals. Attempts were made to catch broods at exactly 3 and 10 days after hatching, but occasional intervention of habitat/weather features broadened the range of capture periods.

At the initial capture (3–4 d old), chicks were marked with permanent markers (Sharpie®) on the ventral surface of the throat in a color pattern allowing individual identification upon recapture. Previous studies of galliform chicks suggest accuracy of this technique is high and its impact on survival, growth, and development is low (J. Carroll, unpubl. data.). Chicks were then weighed and released as described below.

We conducted second captures 10–12 d after hatching for surviving broods to determine if mixing of individuals among different broods had occurred. We recorded the presence or absence of mark combinations from prior captures for each chick. We marked all chicks using a patagial wing band to permit identification at future capture occasions. Chicks were then weighed and released.

Upon completion of capture and marking, chicks were released as a group ≤5 m from the attending adult, as determined by radio-telemetry, and the chicks usually immediately began their "lost" call (Stoddard 1931). Radio-tagged adults flushed by the capture procedure remained within 5–10 m of the capture site, uttering the "scatter" or "alarm" call (Stoddard 1931). Within 5–10 min following release, all calling ceased and the radio-collared adult(s) moved away from the capture location.

Computation of brood amalgamation rates. We computed minimum percent brood amalgamation by dividing the number of broods known to have been amalgamated by the total number of broods captured at each capture period (initial or second). Broods were recorded as known amalgamations when any chick possessed mark combinations originating from another brood or when multiple chicks (≥4) completely lacked mark combinations. To be conservative, we only applied the latter criterion to second captures (10–12 d) where first captures of the brood were recorded as complete, and we assumed that broods containing multiple individuals meeting this criterion were the result of amalgamations and not the result of incomplete captures.

We computed maximum percent brood amalgamation by dividing the sum of known amalgamated broods and broods suspected of exhibiting amalgamation by the total number of broods captured at each capture period. Suspected amalgamation of broods at this capture period was determined by the presence of 1–3 chicks lacking mark combinations, escape by flight of brood members (all captures occurred prior to the period at which chicks could fly), and large differences in body weights of captured chicks. Broods exhibiting large differences in body weights were initially recorded as unknown amalgamations. Following the breeding season, we computed the 99% confidence interval around the mean within-brood variance in body weight using all broods recorded as unmixed. If the mean within-brood variance in body mass of a brood with unknown amalgamation status was outside this 99% confidence interval, we categorized the brood as exhibiting amalgamation.

Minimizing and testing for observer introduced bias. To minimize and investigate the introduction of observer bias to our results, we used several direct methodological and indirect analytical techniques. At all stages of each

Table 1.   Total number of Northern Bobwhite broods captured at each period during 2002–2003, minimum and maximum estimates of brood amalgamation, and distribution of both known and potential amalgamations among classes of attending adults, as determined by radio-location.

Chick age	2002		2003	
	3–4 d	10–12 d	3–4 d	10–12 d
Broods captured	45	29	15	9
Known amalgamations	3	6	0	2
Potential amalgamations	2	9	1	4
Minimum brood amalgamation	6.7%	20.7%	0.0%	22.2%
Maximum brood amalgamation	11.1%	51.7%	6.7%	66.7%
Mixed broods with both sexes	2	9	0	0
Mixed broods located with single adult female	0	0	1	3
Mixed broods with single adult male	1	1	0	0
Mixed broods with ≥2 females	1	1	0	2
Mixed broods with ≥2 males	0	0	0	1
Mixed broods with ≥2 adults	0	2	0	0
Mixed broods with unknown number of adults	1	2	0	0

capture, we listened for the lost call of chicks outside of the enclosure to determine if any individuals had escaped. Captures were recorded as complete if no "lost" calls were heard. Overall success rates for each capture period were computed as the percentage of complete brood captures.

We quantified the return time of captured chicks to the attending adult for a subset of captured broods. We computed the mean time and 95% confidence interval between release of the chicks and their return to the parent, as indicated by a lack of "lost" or "alarm" calls emitted by either chick or parent. Additionally, we computed the mean distance and 95% confidence interval between the chick release area and the adult with which the chicks were captured using data gained from homing via radio-location (Samuel and Fuller 1994).

We predicted that the number of chicks in amalgamated broods, as determined by our entire rule set, would be greater than the number in non-amalgamated broods. Assuming that our techniques did not influence the frequency of brood amalgamation on our study area, we also predicted sizes of broods captured on the study area would be equal to those in a control group. We compared chick count of amalgamated and non-amalgamated broods at each capture occasion using a one-tailed *t*-test for independent samples. We tested for potential effects of multiple captures on overall brood size by comparing second brood captures conducted on the study area to captures conducted on the re-mainder of Tall Timbers during the same time periods using a two-tailed *t*-test for independent samples. Broods outside of the study area were captured once at ages ranging from 9–14 d using the protocol for second captures. Chicks were released following the procedures described above.

RESULTS

During 2002, 157 adult and subadult bobwhite were monitored throughout the breeding season. We conducted 70 captures of 45 distinct broods on the study area. Ninety-two percent of initial captures, recorded as amalgamations upon second capture, were complete. Overall success rates of first and second captures were 86% and 72%, respectively. No broods were placed into the potential amalgamation category as a result of weight measurements. Minimum frequency of brood amalgamation at the first capture period was 6.6% with a maximum brood amalgamation frequency of 11.1% ($N = 45$; Table 1). Minimum to maximum frequency of brood amalgamation for second captures ranged from 20.6 to 51.7% ($N = 29$; Table 1).

During 2003, 102 adult and sub-adult bobwhite were radio-monitored throughout the breeding season. We conducted 24 captures of 15 distinct broods on the study area. Eighty-six percent of initial captures, recorded as amalgamations at the second capture period, were complete. The overall success rates of first and

second captures were 73% and 67%, respectively. Mean variance in non-amalgamated brood weights at the first capture period was 0.32 ($\pm$0.26, $N = 13$). The minimum variance in weight exhibited by one brood placed into the potential amalgamation category was 1.4 for initial captures. Small sample size of non-amalgamated broods at the second capture period precluded computation of variance estimates, and broods having the potential for inclusion in the potential amalgamation category under this criterion were dropped from analysis. Minimum frequency of brood amalgamation at the first capture period was 0.0% with a maximum brood amalgamation estimate of 6.6% ($N = 15$). Minimum to maximum frequency of brood amalgamation at the second capture period was 22.2% to 66.7% ($N = 9$).

Average time of return to the respective parent(s) was 287.0 s ($\pm$59.0, $N = 16$). Captured chicks were released $\leq$5 m of their respective parent(s) (100% $\leq$ 5 m, $N = 16$). During 2002, the mean number of chicks in amalgamated broods was greater than in non-amalgamated broods at 3–4 d of age when first captured (mean = 8.1, 17.8; $t_{4,32} = -2.74$; $P = 0.02$) and at 10–12 d of age at second capture (mean = 5.6, 10.4; $t_{19.6} = -2.52$; $P = 0.01$). During 2003, small sample sizes of first captures did not permit statistical analysis. At 10–12 d of age, the number of chicks was also greater in amalgamated broods (mean = 8.1) than non-amalgamated broods (mean = 4, $t_7 = -1.88$, $P = 0.05$). First captures were not analyzed due to small sample size.

During 2002, no difference was found between the number of chicks per brood at second capture on the study area (mean = 6.3) and chick number per brood captured on the remainder of Tall Timbers (mean = 5.4, $N = 16$, $t_{40} = 0.63$, $P = 0.53$). During 2003, the number of chicks per brood captured was smaller on the study area (mean = 6.8) than on the remainder of Tall Timbers (mean = 10.5, $N = 10$, $t_{17} = -2.59$, $P = 0.02$).

DISCUSSION

Our results suggest a high rate of brood amalgamation in Northern Bobwhites, verifying the anecdotal observations of previous researchers. Our results also demonstrate that brood amalgamation begins early during the brooding period. However, our results are potentially subject to variance introduced by observer bias and the assumptions of capture-recapture marking techniques, namely that brood amalgamation is not being induced as a result of the first capture, that marks were not lost, and that all individuals were marked on first capture.

Violation of the initial assumption could inflate our estimates of the frequency of brood amalgamation. However, our procedural steps showed that chicks rapidly returned to the attending parent(s) upon release. Furthermore, our statistical techniques provide evidence that we were not inducing brood amalgamation on the study area. Support for our initial prediction (sizes of amalgamated broods are larger than non-amalgamated broods) demonstrates that brood size is indicative of brood mixing. In light of these results, the lack of difference among study areas and control group brood sizes suggests that multiple captures did not positively bias brood size. However, this logic is limited by the assumption that brood sizes are an accurate index of the occurrence of brood amalgamation on both areas. Furthermore, it is also possible that observer bias introduced by these procedures occurred at a level below that required for statistical significance.

We realize that the capture of individuals lacking mark combinations could have resulted from incomplete initial captures of brood members. Their inclusion in our computations would have inflated the estimated frequency of brood amalgamation. In order to minimize this potential for inflation, we attempted to partition the uncertainty arising from captures of unmarked individuals by including only those second captures, initially recorded as complete, with $\geq$4 unmarked individuals into the more conservative minimum estimate of brood amalgamation. Methods employing the use of differential body weights to indicate brood amalgamation likely underestimated its frequency because amalgamated broods may contain individuals of the same age and, therefore, weight. Brood amalgamation, as indicated by the minimum rate, represents the most careful and conservative estimate of this behavior among Northern Bobwhites to date. We believe the true frequency of brood amalgamation is within the range of our minimum and maximum estimates. We also believe the maximum

estimate of brood amalgamation is based on sound methodology and, therefore, may be useful for biologists to consider. The utility of each estimate is dependent on its purpose. For example, when estimating survival of chicks within a brood using flush counts, the maximum estimate of brood amalgamation represents an upper bound on the error introduced by this behavior.

Brood amalgamation and its aliases (brood mixing, brood parasitism, creching, gang-brooding) have been viewed as parasitic systems in the past, having distinct benefits for the parasite and costs for the host (Eadie et al. 1988). However, few studies have quantified the costs and/or benefits of this behavior to both donors and recipients, and it is likely that this behavior is more complex than originally believed (Riedman 1982; Eadie et al. 1988). Furthermore, the underlying theory attempting to explain the existence and function of brood amalgamation has been primarily based on various species of migratory waterfowl.

The occurrence of brood amalgamation in Galliformes, however, is a different system, characterized by more limited dispersal ability, a limited degree of spatial movement within and between breeding seasons, and the higher potential for relatedness among individuals caring for mixed broods (Stoddard 1931; Burger et al. 1995; Brennan 1999). Therefore, we believe it is also important to think of brood amalgamation as potentially being affected by factors outside of the host-parasite framework. Mechanisms that include components of kin selection and measures of inclusive fitness may be particularly critical in the investigation of this behavior among Galliformes (Hamilton 1964a,b; Andersson 1984; Grafen 1984).

Mechanisms commonly proposed to explain the "donation" of offspring to other adults include (1a) grouping of "incompletely imprinted" members from different broods following attack or confusion caused by predators or natural factors; (2a) mixing among broods as a consequence of competition for brood habitat between two adults; (3a) donation of young by adults unwilling or unable to provide continued parental care; (4a) donation of offspring to related individuals allowing additional nesting attempts by more experienced/fecund individuals, thereby increasing the inclusive fitness of family groups; and (5a) donation of offspring to the male of the pair allowing the female to renest, potentially increasing fitness of the pair (Munro and Bedard 1977; Eadie et al. 1988). Potential mechanisms explaining the "receipt" of unrelated offspring by an individual include the: (1b) inability of adults to discriminate among unrelated and related offspring, yielding tolerance of extra-brood members; (2b) inability of adults to resist adopting offspring as a result of current or residual hormone levels; (3b) lack of any significant cost caused by the acquisition of unrelated young; (4b) dilution of predation risk for immature individuals through clumping or predator swamping; (5b) parenting experience acquired by helper individuals associated with a particular brood; and, (6b) kidnapping of offspring to reduce predation risk to offspring of the dominant pair (Darling 1938; Taylor 1976; Riedman 1982; Birkhead and Nettleship 1984; Eadie et al. 1988; Heinsohn 1991; Nastase and Sherry 1997).

Hypothesis 1a is called into question as a result of recent research into offspring-recognition illustrating the ability of immature Galliformes (chicken, *Gallus gallus*) to differentiate between known and unknown objects upon which they were imprinted at an early age (Regolin et al. 1995). However, the applicability of this work to Northern Bobwhites is unknown.

Support for hypothesis 2a is lacking, given the gregarious nature of bobwhite (Stoddard 1931; Brennan 1999) and the fact that several ($N = 7$) mixed broods captured during 2002 and 2003 were under the care of multiple (>2) attending adults, indicating that the degree of competition for resources when brooding is likely lower than that for waterfowl (Stoddard 1931; Brennan 1999). However, the relationship between these broods and the attending adults is unknown. Given that the benefit gained by helper individuals is likely low due to the high annual mortality rates and short lifespan of bobwhites, hypothesis 5b also is unsupported (Brennan 1999).

Although our methods provide direct evidence for brood amalgamation in Northern Bobwhites, our results do not adequately test any empirical hypotheses. The frequency and potential causes of brood amalgamation would best be investigated using molecular techniques. Such techniques would allow estimates of the degree of relatedness between offspring and their natural versus adopting parent(s), in ad-

dition to more accurate estimates of the frequency of brood amalgamation (Blouin 2003; Jones and Ardren 2003). The integration of molecular techniques with traditional field approaches (mark-recapture, radio-location) will allow refinement and refutation of hypotheses to explain the occurrence of brood amalgamation among galliform species such as Northern Bobwhites.

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