



*Avian Behavior, Ecology, and Evolution*

## Are adoptions in a predatory songbird a strategy to aid mate acquisition?

### ¿Son las adopciones en un ave canora depredadora una estrategia para facilitar la adquisición de pareja?

Christopher E. Hill<sup>1</sup> , Kyle R. Miles<sup>1</sup> , Katie A. Maddox<sup>1</sup> and Amy Tegeler<sup>2</sup>

**ABSTRACT.** Adoption of unrelated young by adult birds is costly and therefore they should avoid it unless adoption carries compensating benefits. Loggerhead Shrikes (*Lanius ludovicianus*) have a monogamous mating system with low rates of extra-pair paternity and biparental care of young. To date, no documented instances of adoption have been published in this species. In two small nesting populations in South Carolina, we documented six cases in three years in which an unpaired Loggerhead Shrike adopted a brood of apparently unrelated nestlings or fledglings, in some cases sharing provisioning duties with the brood's mother and in two cases taking over care completely while the mothers renested with different males. These adoptions occurred in 3.4% of all nesting attempts and in about 5% of broods that reached the nestling or fledgling stages. In at least five of the adoptions, young survived to independence. All adopters were male, and we documented a male-biased sex ratio among unpaired birds. We surveyed other Loggerhead Shrike researchers and uncovered three instances of similar alloparental care in three other populations, suggesting that this behavior is widespread but previously overlooked. We speculate that adoption by male Loggerhead Shrikes may be adaptive in male-biased populations by increasing the chances of an adopting male subsequently mating with the mother of the chicks he adopted, which happened in two of the six cases we studied, though in one case with a year's delay. This behavior should be sought in other populations of shrikes and other avian lineages.

**RESUMEN.** La adopción de crías no emparentadas por parte de aves adultas es costosa y, por tanto, deberían evitarla, a menos que la adopción conlleve beneficios compensatorios. Los Alcaudones Americanos (*Lanius ludovicianus*) tienen un sistema de apareamiento monógamo con bajas tasas de paternidad extrapareja y cuidado biparental de las crías. Hasta la fecha, no se han publicado casos documentados de adopción en esta especie. En dos pequeñas poblaciones nidificantes de Carolina del Sur, documentamos seis casos en tres años en los que un Alcaudón Americano no emparejado adoptó una nidada de polluelos o volantones, aparentemente no emparentados, en algunos casos compartiendo tareas de aprovisionamiento con la madre de la nidada y en dos casos asumiendo el cuidado por completo mientras las madres renidificaban con machos diferentes. Estas adopciones se produjeron en el 3,4% de todos los intentos de nidificación y en aproximadamente el 5% de las nidadas que alcanzaron las fases de polluelos o volantones. En al menos cinco de las adopciones, las crías sobrevivieron hasta la independencia. Todos los adoptantes eran machos, y documentamos una proporción de sexos con sesgo hacia ese sexo entre las aves no apareadas. Hemos consultado a otros investigadores del Alcaudón Americano y hemos descubierto tres casos de cuidado aloparental similar en otras tres poblaciones, lo que sugiere que este comportamiento está muy extendido pero que hasta ahora se había pasado por alto. Especulamos que la adopción por parte de machos de Alcaudón Americano puede ser adaptativa en poblaciones con sesgo hacia los machos al aumentar las posibilidades de que un macho adoptante se aparee posteriormente con la madre de los polluelos que adoptó, lo que ocurrió en dos de los seis casos que estudiamos, aunque en uno de ellos con un año de retraso. Este comportamiento debería buscarse en otras poblaciones de Alcaudones y otros linajes de aves.

**Key Words:** *adoption; alloparental care; fledgling; Lanius ludovicianus; Loggerhead Shrike; nestling; tertiary sex ratio*

#### INTRODUCTION

Parental care in birds, especially those with altricial young, is essential but costly, leading to trade-offs between effort expended in current reproduction and potential for future reproduction (Roff 1992). The costs to adult birds of raising young not their own are emphasized by the existence of infanticide, not adoption, by replacement mates in some circumstances (Rohwer 1986). Nonetheless, adoption of unrelated young has been found in over 150 bird species (Riedman 1982), and there has been much interest in explaining this evolutionary quandary: young birds may increase their fitness by seeking out adoptive parents (Pierotti 1987), but why would adults engage in a costly behavior to support unrelated individuals? Proximate explanations for adoptive behavior often ascribe adoptions to errors of discrimination by adopting adults (Riedman 1982). Such errors are made more

likely by hormonal priming on account of a parent currently having (Stutchbury and Ogden 1996) or recently having lost (Jouventin et al. 1995) dependent young of similar age to the prospective adoptee. Adults without young of their own should both be less hormonally primed for parental care and less likely to mistake a potential adoptee for their own chick. Adoptions due to errors in chick recognition should also be promoted by the frequent encounters with unrelated young associated with colonial nesting and by young that are likely to leave their natal territory to beg from adults on neighboring territories (Graves and Whiten 1980). There may also be features of dispersing young that may make them less identifiable, such as movements, voice changes, and sheltering behavior in the immediate post-fledging period, that promote adoption due to failed discrimination by the adopter (Stutchbury and Ogden 1996). On the other hand,

<sup>1</sup>Coastal Carolina University, <sup>2</sup>South Carolina Department of Natural Resources

features that make discrimination easier and should make accidental adoptions less likely are low-density, non-colonial nesting, young that remain on their home territory, and young uniquely identifiable by appearance and voice (Medvin et al. 1993).

Ultimate explanations for why selection has not eliminated errors in chick care recognize the difficulty in evolving mechanisms to reject a begging youngster in one's own nest because such mechanisms would also likely increase the probability of non-adaptive rejection of the adult's own young (Lotem 1993). Even among birds frequently parasitized by specialized brood parasites, rejection of parasite chicks has been notably slow to evolve (Grim 2006). Other ultimate hypotheses allow for the possibility that in some cases adoption could, despite the costs, provide a net benefit in current or future reproduction. In waterfowl with precocial young, adoption has been hypothesized to benefit hosts by reducing predation on the host's young. Such a benefit might outweigh the relatively low cost of adding one more self-feeding precocial chick to a brood (Kalmbach 2006). Even in songbirds with altricial young that require more intensive parental care, adoptive behavior could theoretically increase an individual's current or future reproduction in several ways: larger broods could, in special circumstances, have positive effects on current or future reproduction, as in the case of cooperatively breeding White-winged Choughs (*Corcorax melanorhamphos*; Heinsohn 1991); apparent adoptions might actually involve care of one's own relatives, as in Common Gulls (*Larus canus*) that have such high natal philopatry that adopting a neighbor might mean providing care to a relative (Bukacinski et al. 2000); or adoption could be a route to obtaining a mate and perhaps also to increasing the reproductive value of that mate. It has also been suggested that male birds might adopt young from other nests if the males were likely to have fathered the young through extra-pair fertilizations (Stutchbury and Ogden 1996, Santema and Kempenaers 2021). While a kin selection scenario may commonly occur in the context of helpers at the nest (Varian-Ramos and Webster 2012), empirical support for care for extra-pair young is difficult to obtain (but see Gray 1997), and only recently has a convincing case been made for male Blue Tits (*Cyanistes caeruleus*) optimizing fitness by caring for potential extra-pair offspring (Santema and Kempenaers 2021). Another adaptive scenario is that adopting might increase the odds of acquiring a future mate and might also, by relieving the burden of parental care from that future mate, increase that mate's reproductive value (Rohwer 1986, Meek and Robertson 1991). Adopting to acquire a future mate, often in the context of mate replacement (Rohwer 1986), would be expected to be most common where tertiary sex ratios are skewed, and mating opportunities are correspondingly scarce for one sex.

Shrikes (Laniidae) are a family of 34 species of predatory passerine songbirds in two genera: *Lanius* (32 species) and *Eurocephalus* (two species; Winkler et al. 2020). Four shrike species in the African tropics are cooperative breeders: one of the two *Eurocephalus* and three *Lanius* (Zack and Ligon 1985, Yosef and ISWG 2020c, 2021a, 2021b). Cooperative breeding is suspected in three other Afrotropical shrike species based on limited observations (Yosef and ISWG 2020a, 2020b, 2020d). At least 27 of the 32 *Lanius* species, however, and all north temperate zone shrikes are socially monogamous, though in one of those,

the Red-backed Shrike *Lanius collurio*, unmated birds may very occasionally help rear young of a mated pair (Yosef et al. 2020).

Loggerhead Shrikes, *Lanius ludovicianus* (hereafter, shrikes) are medium-sized (approximately 50 g) shrikes found across most of North America. Shrikes in the southeastern United States have an extended nesting season (about February–July), can successfully raise two broods in a season, and frequently renest both after nest failures and after successful nesting attempts (Gawlik and Bildstein 1990, Yosef 1992). Only females develop brood patches and incubate (Miller 1931, Pyle 1997). Shrikes form monogamous pair bonds, and pairing status is straightforward to determine in the breeding season: females and males associate closely starting in January in South Carolina (C. Hill, *personal observation*), males feed females during courtship, laying, and early incubation, and males often attend the nest closely while the female is incubating (Yosef 2020). Both males and females scold humans who closely approach a nest that holds chicks (Lohrer 1974). Extra-pair paternity has been quantified in Loggerhead Shrikes as involving less than 4% of offspring (Etterson 2004). In the first few days after chicks hatch, males forage for the entire family, bringing food to females who then transfer it to the young (Yosef 2020). Later feeding of nestlings and fledglings is by both parents (Gawlik et al. 1991). After fledging a first brood, a female may renest while the fledglings are still dependent on parents for food. In this case the male takes over feeding all the fledglings and may also feed the female (Yosef 1992, Woods 1994).

In the course of studying the population biology of two nesting populations of Loggerhead Shrikes in South Carolina, we took advantage of individually marked birds to track the nesting and provisioning behavior of up to 36 pairs a year in some detail. This allowed documentation of alloparental care and monitoring of the outcomes to adopting adults, the young they adopted, and the original parents of the adopted young.

## METHODS

This study was carried out in two resident populations in South Carolina, United States. From 2018–2020, two observers monitored 13–32 shrike territories at three study sites in Horry County on the coastal plain (center of study area 33°45' N, 78° 58' W), while in 2019 and 2020 a third observer monitored 6–8 territories in Richland County in the South Carolina midlands (34°2' N, 80°56' W). Adults were trapped with box traps, and each individual received a unique combination of color bands. Sex of adult shrikes was assigned by brood patch (Pyle 1997) or breeding behavior or tentatively assigned by plumage (Sustaita et al. 2014, Morgan and Chabot 2020). We did not find cloacal protuberances to be reliably detectable in males. All plumage-based sexing was later confirmed by breeding behavior when possible. To determine the sex ratio of unpaired birds, we mapped all territories in April and May of each year and recorded each unpaired bird's sex as male, female, or unknown.

Each territory in Horry County was visited at least weekly to determine pairing status and discover any nesting attempts, and territories in Richland County were checked at least every 10 days. Nests were usually found during incubation, occasionally during nest-building or the nestling phase. To infer the date of nest initiation (the day the first egg was laid), we assumed 17 days of incubation and one egg laid per day, with incubation commencing

**Table 1.** Characteristics of adopting Loggerhead Shrike (*Lanius ludovicianus*) adults and the broods they adopted, including outcomes for each, during six adoptions of Loggerhead Shrike broods in South Carolina, United States.

Year and adopter	Adopter's sex	Adopter's age	Chick count and stage	Outcome for brood	Outcomes for adopter <sup>†</sup>
2019 rmgg	Male	1	Nestlings <sup>‡</sup>	Survival to independence	Territory, mate, bred next year
2019 myaa	Male	≥2	2 fledglings	Survival to independence	Territory, mate, bred same year
2019 gmrr <sup>§</sup>	Male	≥2	2 nestlings	Survival to independence	Territory and mate
2020 ygmr	Male	≥2	4 nestlings	Survival to ≥29 days	Territory and mate
2020 mbyg <sup>§,  </sup>	Male	1	2 fledglings	Survival to independence	Territory
2021 mbyg <sup>  </sup>	Male	≥2	2 fledglings	Survival to independence	(none)

<sup>†</sup> “Territory” means acquired a territory concurrently with adopting, “mate” means the male paired with the mother of the adopted chicks at least for the duration of the adoption, “bred” means initiated a new nest with the mother of the adopted chicks.

<sup>‡</sup> Nest was too high to get a count of chicks.

<sup>§</sup> The same nesting pair produced the two broods adopted by these two different males in two different years.

<sup>||</sup> mbyg adopted in two consecutive years: in 2020, one complete brood; in 2021, two partial broods, one fledgling each from two different broods, simultaneously.

on the day the penultimate egg was laid (Yosef 2020). When we did not observe hatch dates, we inferred them from the appearance of the nestlings (Lohrer 1974) or, for unreachable nests, by counting back 19 days from the day of fledging. Chicks in Horry County were banded in the nest at 10–14 days old, with nest-specific (2018, 2019) or individual-specific (2020) color combinations. Except for one nest, chicks in Richland County were not banded in the nest, but many were color banded as fledglings. Following Chabot et al. (2001) and Luukkonen (1987), we considered fledglings to have achieved independence from parents if they survived to 40 days post hatch, though fledglings in our population often remained on their natal territory past 60 days of age.

The observations reported below came during a study of population processes, and quantifying parental provisioning behavior was not originally a focus of our study. Nonetheless, observations of associations between adults and dependent fledglings were made in all three years at essentially all nests. We defined adoption as any instance where an adult that had not been present for the initiation of a nesting attempt (including the female's fertile period) cared extensively or exclusively for the young from that nest. This criterion excluded one-time feedings by an adult of a wandering fledgling from a nearby nest (which we only observed one time in three years). Because parental provisioning was not a focus of the overall study of shrikes, we did not quantify the rates of feeding by adoptive parents until the latest three cases.

We shared our observations with members of the Eastern Loggerhead Shrike Working Group and asked if they had observed any similar events. We used responses to this to add to our understanding of the circumstances of shrike adoptions but excluded them from calculations of frequency of adoption.

## RESULTS

Between Horry and Richland Counties, we followed 27–36 breeding pairs of shrikes at any given time. We documented 176 nesting attempts, with 153 in Horry and 23 in Richland. Seventy-seven percent of these nests hatched, 52% produced fledglings, and about two-thirds of the subset of fledged broods tracked in detail (C. Hill, *unpublished data*) had at least one fledgling survive to independence. Unpaired birds varied from 9%–18% of territorial birds in Horry County in April and May. The male to

female ratio of known-sex unpaired birds was 24:2. Five additional unpaired birds could not be sexed.

We observed six clear instances of adoption, summarized in Table 1, including one male (“mbyg” in 2021, last line in Table 1) who simultaneously adopted fledglings from two different nests. Adoptions occurred in 3.4% of nesting attempts and in about 5% of nests that were in the nestling and fledgling phases. For all six adoptions, we observed at least two weeks of close association between adopting adults and the adopted young (range 16–100 days, average 44, SD = 29). The original males had disappeared from four nests at the time adopters took over care of the young. For three additional host nests, the original males were still present on the study site at the time of the adoption, usually on or adjacent to the nesting territory. Two of those remaining males were caring for older fledglings; one who was not caring for any young disappeared soon after his young were adopted. It is possible that our calculation of adoption frequency is conservative: we note here but will not further discuss two additional cases where an outside male replaced the original male of a pair during a nesting attempt but where we could not determine the timing of the replacement precisely enough to class them as adoptions (i.e., the replacing male might have been present during the female's fertile period).

All adopting adults in the South Carolina populations were male. We documented three adoptions during the nestling phase and three in the fledgling phase but none during incubation. In at least five of the adopted broods, at least one chick survived to independence and, in the sixth, the fledglings were documented to have survived to at least 29 days old, though we could not locate the adopter or fledglings a week later. The outcomes for the adopting males included acquisition of a new territory (five of six adoptions), pairing with the mother of the adopted brood (four cases), and breeding with the mother of the adopted brood (by two males—one in the year of the adoption, the other not until the following year). The same male, mbyg, adopted two different broods from different territories in different years (Table 1, lines five and six), each time raising someone else's fledglings by himself (that is, without pairing with the mother), and in the second case he cared for, at the same time, one fledgling each from two different nests (counted as a single adoption for the male, last line of Table 1). Also, a single breeding pair had two different broods adopted by different males in different years (Table 1, lines

**Table 2.** Provisioning of adopted Loggerhead Shrike (*Lanius ludovicianus*) offspring by adopting males and mothers in South Carolina, United States.

Year and adopter	Observation date	Offspring stage	Offspring age (days)	Observation duration (min)	Feeds by adopting male	Feeds by mother
2020 ygmr	19 June	Nestlings	10	60	12	29
2020 ygmr	1 July	Fledglings	22	60	8	3
2020 mbyg	30 May	Fledglings	58	10	5	0 <sup>†</sup>
2021 mbyg	24 May	Fledglings	39	30	4	0 <sup>†</sup>

<sup>†</sup> No mother was present; mbyg was caring for both these broods by himself.

three and five). Although we could not monitor territories constantly and no doubt missed interactions, it is still notable that in mbyg's adoptions (last two lines of Table 1), he had no observed close associations with the mother of the chicks. In each of those cases the mothers were associating with other males while mbyg cared for their offspring by himself. We quantified provisioning behavior in three of the cases, and those data are reported in Table 2.

Three members of the Eastern Loggerhead Shrike Working Group offered examples that would also meet our criteria for adoption: one instance in Indiana where an adopting male fed fledglings (A. Kearns, Indiana Department of Natural Resources, *personal communication*), one in Ontario, Canada where an adopting male took over exclusive care of a brood of nestlings (A. Chabot, African Lion Safari, *personal communication*), and one in Arkansas where a male moved to pair with a female who had fledglings and took over feeding and guarding the dependent fledglings (E. Donahue, Arkansas State University, *personal communication*). As with the South Carolina adoptions, all the adopters were males.

## DISCUSSION

We have reported on the first documented instances of adoption in Loggerhead Shrikes, with circumstances that argue strongly against errors of discrimination and include instances of adoption during the fledgling phase, rarely observed in any songbird (Wysocki et al. 2018). We hypothesize that there may be an adaptive function of adoption by male Loggerhead Shrikes in mate acquisition in a male-biased population.

The circumstances of the adoptions argue against mistaken identity: in four of six cases, the adopting shrikes moved to the natal territory of the young birds they adopted and took over broods of nestlings and fledglings without any apparent prior connection to the broods, and in no case was there evidence that the adopting birds had chicks of their own. Although we have systematic observations of feeding behaviors for only three of these adoptions, all adopted broods apparently received more than adequate care from the adoptive parent because at least one individual of five broods survived to independence (and the sixth brood survived a minimum of 23 days after the adoption), this despite fewer than half of shrike broods in this and similar populations (Yosef and Grubb 1994) reaching independence. Renesting females do not provide care for already fledged young from previous broods (Yosef 1992, Woods 1994), and the survival of the adopted young even when their mother renested also indicates that the adopting males were feeding the young.

Though we do not have molecular samples with which to assess relatedness, kin selection seems unlikely to be involved. Four of the six adoptions were by birds never before seen on our study sites. Furthermore, the only previous study of extrapair fertilizations in this species found very low extrapair paternity (Etterson 2004).

We speculate that males who adopt may gain fitness by acquiring a territory and increasing their chances of mating, and that male competition for mates is enhanced by a male-biased tertiary sex ratio (92% of known-sex, unpaired birds on our study site were males). All five of the adopting males acquired a territory overlapping with or adjoining the territory where they adopted. One male nested with the mother of the adopted young in the same season as the adoption, and another male nested with the mother in the next season. However, we note that one male, mbyg, gave up most of two breeding seasons caring for the offspring of others with no offspring of his own to show for it, so the fitness benefits of this rather extreme investment in adoption certainly are speculative. We cannot evaluate the trade-offs because we have no way of measuring the eventual breeding success of males on the move in the breeding season who have the opportunity to adopt but choose not to.

If adoption is this regular in Loggerhead Shrikes, why has it remained undocumented until now? Or conversely, if adoption is generally rare, why have we found it so frequently in South Carolina? Three percent of all nesting attempts led to an adoption, 5% of broods that reached the nestling or fledgling stage ended in adoption, and, because adopted broods survived particularly well, approximately 1 in 10 young raised in these populations in these three years was cared for by an adoptive parent. One possibility is that, because the shrikes at both our study sites are in an urban rather than agricultural landscape, road mortality (Flickinger 1995) or some other unknown effect of urban living may affect the breeding system, perhaps by increasing adult mortality and creating openings for replacement males. However, high turnover in adults does not by itself explain why replacement males would care for young so readily (Rohwer 1986), especially in mbyg's cases (lines 5 and 6 in Table 1) where the male was never even paired to the parental female (i.e., he was twice a replacement father to fledglings but never a replacement mate to a female). Another possibility is that this study population was uniquely suited to document a phenomenon that may be present more widely than is recognized because (1) we were able to individually identify nearly every adult in the population, (2) we monitored a large enough sample of nests intensively enough to reveal this behavior even though that was not our original focus (c.f. Santema and Kempnaers 2021), (3) at this latitude shrikes routinely have



multiple nesting attempts per season, and (4) based on persistence of banded birds (C. Hill, *unpublished data*), there is much less movement and mixing in these populations than in migratory Loggerhead Shrike populations (Haas and Sloane 1989, Collister and de Smet 1997). Because of (3) and (4), a male in this population will have more opportunities to encounter and mate with a female in the current or following year after adopting her young. Support for the idea that alloparental care is not confined to this population but is widespread in Loggerhead Shrikes comes from anecdotes from three colleagues working with (non-urban) shrike populations in other parts of the continent. Since adoption has now been documented in Loggerhead and Red-backed Shrikes (Yosef et al. 2020), it should be looked for more widely in other species of shrikes and in other avian species with altricial young.

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#### Author Contributions:

C.E.H. and A.K.T. initiated the study. All four authors collected data with K.R.M. documenting most of the adoptions and A.K.T. providing the most data on provisioning. C.E.H. wrote the paper.

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#### Data Availability:

Data/code sharing is not applicable to this article because no data code beyond data included in the text were analyzed in this study.

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