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Letter to Editor

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Conspecific nest-raiding directs more at dominant breeders in the azure-winged magpie

Lifang Gao [a], Xiaodan Zhang[a], Tianchang Yang[b], Shaoxue Wang[b], Qian Wang[a], Fangyuan Liu[a], Zhenqin Zhu[a], Shumei Zi[a], and Bo Du[a,*]

[a]School of Life Sciences, Lanzhou University, Lanzhou, Gansu 730000, China and [b]Cuiying Honors College, Lanzhou University, Lanzhou, Gansu 730000, China

*Address correspondence to Bo Du. E-mail: dubo@lzu.edu.cn.

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Conspecific animals in the wild use limited resources—such as food, nest site, and mating opportunities—very differently (Shuster and Wade 2003), which has been widely considered a consequence of phenotypic diversity (Shuster 2010). For instance, breeding individuals that carry superior phenotypes generally have higher resource holding potential (RHP) and are therefore more likely to amass more resource and realize higher reproductive success than those with lower RHP (Hurd 2006; Kelly 2008). Due to the dominance of superior phenotypes' carriers in resource competition, it is quite natural to take for that superior phenotypic traits will expand rapidly in a population. However, such a phenomenon rarely occurs in nature (Shuster 2010), implying that there must be some negative evolutionary forces that antagonize the dominance of superior phenotypes. In many animal species, adverse social or environmental factors (such as antisocial behaviors directed by conspecific competitors at each other) can reduce the reproductive output of breeding individuals via a negative effect on offspring's survival (Ridley 2007). Therefore, it can be hypothesized that antisocial competitive behaviors may play a key role in preventing superior phenotypic traits from expanding excessively. We tested this hypothesis in the azure-winged magpie *Cyanopica cyanus* that breeds on the Tibetan Plateau, by investigating their conspecific nest-raiding behaviors (i.e., an individual stealing either eggs or chicks from the nests of other breeding individuals). Limited by the shrub-nesting character of breeding individuals and the cluster distribution of shrubs on the alpine meadow, the Tibetan population of azure-winged magpie was divided into a string of separate colonies. In each colony, breeders constructed their nests in a highly clumped pattern (20–180 nests ha^{-1}; Ren et al. 2016). Under this circumstance, breeding individuals compete over nest site and mating opportunities intensely (Gao et al. 2021) and conspecific nest-raiding events occur frequently (Ren et al. 2016). Since conspecific nest-raiding can reduce the reproductive output of victim individuals, if it is directed more at dominant breeding individuals that can amass more resources and produce more offspring than subordinate ones, the hypothesis will be supported that antisocial competitive behaviors act as a reverse evolutionary force of superior phenotypes. Otherwise, it will provide no evidence for this hypothesis in the Tibetan population of azure-winged magpie.

Based on 10-year data about the breeding ecology and adult behaviors in the Tibetan azure-winged magpies (material and methods are provided in the Supplementary Data), we addressed: (1) which nests in the Tibetan population were more likely to be raided by conspecific individuals and (2) the effect of conspecific nest-raiding on the reproductive success of raided individuals. In total, we monitored 608 azure-winged magpie nests that successfully fledged at least one offspring. More than one-third of these nests (207 nests) were raided at least once by conspecific individuals (Figure 1A). Approximately 8% (189 of 244) of conspecific nest-raiding events occurred at the first half of the breeding season. Behavioral data extracted from adults' provisioning videos showed that the majority of conspecific nest-raiding (19 of 21 cases) was carried out by later-breeding individuals. The age of raiders (2.21 ± 0.43, $n = 14$) did not differ significantly from that of females (2.64 ± 1.08; $t = 1.31$, df $= 13$, $P = 0.21$) and males in the raided nests (2.57 ± 1.02; $t = 1.10$, $df = 13$, $P = 0.29$); however, their nest commencement dates (12.05 ± 4.27 d, $n = 21$ nests) were significantly later than that of raided nests (7.57 ± 3.85 d; $t = 7.56$, $df = 20$, $P < 0.001$). Comparisons in offspring numbers between raided and un-raided nests showed that raided nests produced significantly more eggs at the beginning of reproduction (6.16 ± 1.12, $n = 207$ nests) than un-raided nests (5.41 ± 1.12, $n = 401$ nests; $t = 8.50$, $df = 606$, $P < 0.001$), however, their fledgling number (4.14 ± 1.36, $n = 207$ nests) was significantly lower than that of un-raided nests (4.40 ± 1.39, $n = 401$ nests; $t = 2.50$, $df = 606$, $P = 0.013$; Figure 1B). The results of fitting generalized linear mixed models indicated that both the probability and the times of a nest being raided by conspecific individuals were quite closely related to clutch size but not highly correlated to nest commencement date

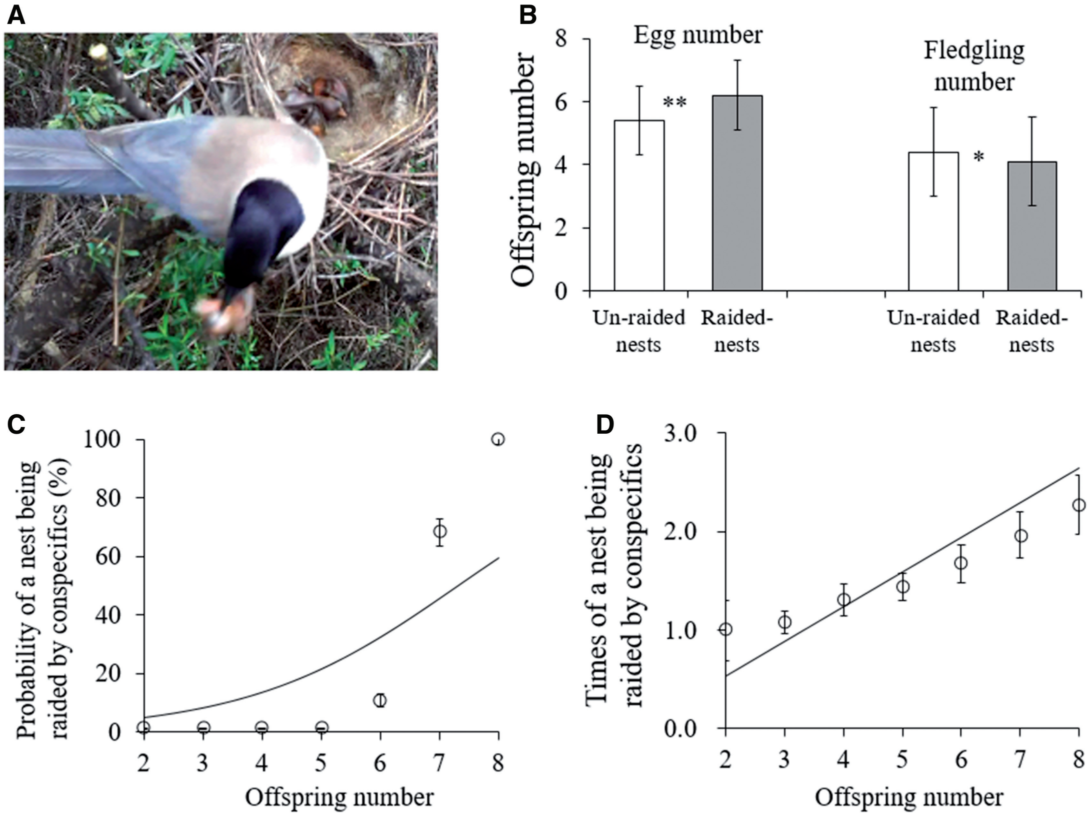

Figure 1. One conspecific nest-raiding event occurred in the Tibetan population of the azure-winged magpie, showing a raider was stealing a chick from a victim nest (A), the comparisons between raided and un-raided nests in their egg and fledgling numbers (B), and the probability (C, $R^2 = 0.70$, $F_{1,5} = 11.71$, $P = 0.019$) and the number of times (D, $R^2 = 0.81$, $F_{1,4} = 6.67$, $P = 0.015$) that an azure-winged magpie nest was raided by conspecifics.

Table 1. Fitting generalized linear mixed model to test the effect of clutch size and nest commencement date on the probability that an azure-winged magpie nest was raided and the number of times that the nest was raided by conspecific individuals

Model parameters	Probability of a nest being raided				Times of a nest being raided		
Fixed effects	$\beta \pm SE$	n	z	P	$\beta \pm SE$	n	t
Intercept	−4.18 ± 1.38	608	−3.03	0.002	−0.16 ± 1.04	207	−0.16
Clutch size	0.57 ± 0.22	608	2.55	0.01	0.25 ± 0.16	207	2.13
Nest commencement date	−0.02 ± 0.07	608	−0.28	0.78	0.04 ± 0.05	207	0.84
Clutch size × nest commencement date	0.01 ± 0.01	608	0.52	0.60	−0.01 ± 0.01	207	−1.21
Random effects	Variance ± SD	n	VCA results		Variance ± SD	n	VCA results
Year	0.19 ± 0.44	608	20.75%		0.03 ± 0.17	207	3.42%
Colony	0.04 ± 0.19	608	3.84%		0.02 ± 0.13	207	1.99%
Residual	0.69 ± 0.26	608	75.41%		0.83 ± 0.91	207	94.42%

VCA, variance component analysis. When t-values range outside the scope of −1.96 – 1.96, it was considered to reach a significant level.

(Table 1) and that the effect of nest commencement date on the correlation between clutch size and dependent variables did not reach a significant level (clutch size × nest commencement date > 0.05; Table 1). Concerning random effects, both the year and identity of colony made smaller contributions to the variance of dependent variables than did fixed effect variables (Table 1). Consequently, it indicated that the more eggs the nest produced, the higher the probability (Figure 1C), and the larger the number of times (Figure 1D) that it would be raided by conspecific individuals.

Our findings in the Tibetan population of azure-winged magpie indicated that conspecific nest-raiding behaviors had been directed more at dominant breeders than at subordinate ones. In most avian species, breeding individuals with superior phenotypes tend to commence their reproduction earlier than those with average phenotypic traits (Verhulst and Nilsson 2008). It is also the case for the Tibetan azure-winged magpies, in which old, experienced breeders possess apparent dominance in occupying territory and pursuing extra mating opportunities, and they also arrive at the breeding site and start reproduction earlier than young, inexperienced breeders (Gao et al. 2021). Therefore, early-breeding individuals are probable the dominant breeders that can produce larger clutches, and accordingly, later-breeding individuals are subordinate breeders that have produced relatively smaller clutches.

Given that most conspecific nest-raiding events were carried out by later-breeding individuals, it implies that those nest-raiders are probably the subordinate breeders. As the nests that had produced more eggs (i.e., dominant breeders' nests) were more likely to be raided by conspecifics (Figure 1C, D), their reproductive output decreased significantly compared with that of un-raided nests (Figure 1B). As a result, the variation in offspring number between dominant and subordinate breeders became more balanced at the end than that at the beginning of the reproduction. In another word, conspecific nest-raiding prevents the phenotypic traits of dominant individuals from rapid expanding in the Tibetan population of azure-winged magpie. In this sense, although conspecific nest-raiding behaviors belong to various types of conspecific competition over resources, they display an obvious difference from other competitions, such as intraspecific cannibalism in some passerine birds (Parsons 1971; Watanuki 1988) or resource competition (Kelly 2008), where dominant individuals often outcompete subordinate competitors. However, when conspecific nest-raiding occurs, dominant breeders in the Tibetan azure-winged magpies often become the victims. Therefore, our findings provide evidence for the hypothesis that adverse conspecific competitions can become a reverse evolutionary force to superior phenotypes.

Author Contributions

L.G. collected the life-history data in the field and performed the statistical analysis. X.Z., T.Y., and S.W. collated the data. Q.W., F.L., Z.Z., and S.Z. collected life-history data in the field. B.D. organized this study and wrote the manuscript.

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Conflict of interest

The authors declare no conflicts of interest to any other affiliations or persons.

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