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AUTHOR CONTRIBUTIONS

Conceptualization, L.S. and U.B.; Formal Analysis, H.Z., U.B., and L.S.; Visualization, H.Z. and L.S.; Writing — Original Draft, H.Z., L.S., and U.B.; Writing — Review & Editing: H.Z., L.S., and U.B.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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The ‘after you’ gesture in a bird

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Gestures are ubiquitous in human communication, involving movements of body parts produced for a variety of purposes, such as pointing out objects (deictic gestures) or conveying messages (symbolic gestures)[1]. While displays of body parts have been described in many animals[2], their functional similarity to human gestures has primarily been explored in great apes[3,4], with little research attention given to other animal groups. To date, only a few studies have provided evidence for deictic gestures in birds and fish[5–7], but it is unclear whether non-primate animals can employ symbolic gestures, such as waving to mean ‘goodbye’, which are, in humans, more cognitively demanding than deictic gestures[1]. Here, we report that the Japanese tit (*Parus minor*), a socially monogamous bird, uses wing-fluttering to prompt their mated partner to enter the nest first, and that wing-fluttering functions as a symbolic gesture conveying a specific message (‘after you’). Our findings encourage further research on animal gestures, which may help in understanding the evolution of complex communication, including language.

Japanese tits nest in tree cavities with a small entrance, and males and females enter the nest one at a time. We noticed that Japanese tits carrying a food item often fluttered their wings in front of their mates when they were also perched near their nest cavity with a food item (Figure 1A and Video S1). We hypothesized that this visual display functions as a gesture that prompts mates to enter the nest first. Following previous animal studies[4,6,7], we define gestures as movements of a body part that are expressed in the presence of the target recipient, are goal-directed — i.e., a signaler waits for a response after the signal has been produced — do not act as a direct physical agent and receive a specific response.

First, we observed 321 nest visitations to feed nestlings by male and female Japanese tits that were breeding using nestboxes (16 individuals, 8 pairs).

We found that parents adjusted wing-fluttering according to social contexts: they exhibited wing-fluttering when they encountered their mate at the nest site (defined as within five meters of the nestbox) but never when they arrived at the nest site alone (Figure 1B; Generalized Linear Mixed Model: $N = 321$, $Z = 5.35$, $p < 0.0001$). There was a significant effect of sex on wing-fluttering behavior (Figure 1B; $N = 321$, $Z = -2.39$, $p = 0.017$). Six out of 8 females exhibited wing-fluttering, accounting for 14% (24/169) of all nest visitations and 42% (24/57) of nest visitations when accompanied by a mate. In contrast, only one out of eight males displayed wing-fluttering, accounting for 1% (2/152) of all nest visitations and 6% (2/33) of nest visitations when with a mate. In all observed cases (26/26), the tits performed wing-fluttering with their chests facing their mates from a location that should be visible to their mates. In most cases (23/26), they ceased wing-fluttering after their mates had entered the nestbox.

Next, we analyzed the effect of wing-fluttering on the order of nest entry. As most wing-fluttering was observed in females, we focused on nest visitations by females that encountered a male before entering their nestbox ($N = 57$). When females fluttered their wings, males usually entered their nestbox before the females (Video S2). However, when females did not flutter their wings, they usually entered the nestbox before males (Figure 1C; GLMM: $N = 57$, $Z = 3.50$, $p = 0.0005$). For 23% (13/57) of the visitations, females arrived at the nest site first and stayed on a perch until the male arrived, whereas for 77% (44/57) of the visitations, males arrived at the nest site first. However, the order in which parents arrived at the nest site did not affect the order in which they entered the nest ($N = 57$, $Z = -1.14$, $p = 0.25$).

A more detailed analysis revealed that females’ wing-fluttering shortened the latency of males to enter the nest cavity, i.e., the delay between the time when males encountered females at the nest site and the time when the males entered (Figure 1D; Cox mixed-effects model: $N = 33$, $Z = 2.92$, $p = 0.0035$). The order of arrival by males (first arrival: 15/33) and females (first arrival: 18/33) did not have a significant effect on the male’s latency to enter the nest ($N = 33$,

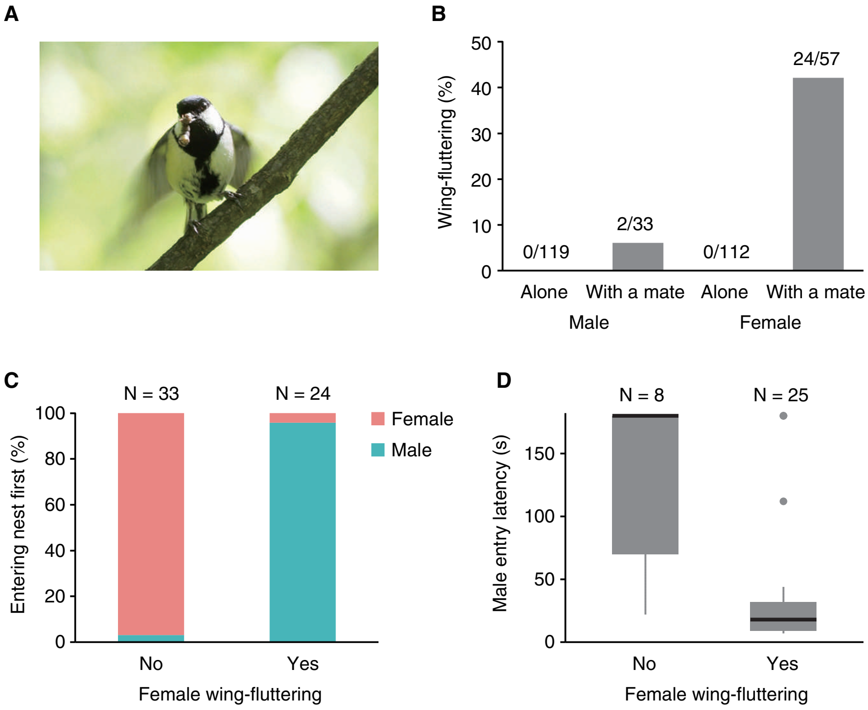

Figure 1. Gestural communication in Japanese tits.

(A) Wing-fluttering by a female Japanese tit. (B) Percentage of nest visitations in which parents exhibited wing-fluttering behavior in relation to social contexts and sex. Note that the number of nest visitations by males and females differed in the "with a mate" context, as there were cases where one parent made multiple nest visitations while the other stayed outside the nestbox with a food item. (C) The order of nest entry (percentage of nest visitations in which each sex entered the nest first) in relation to females' wing-fluttering. Data were derived from the nest visitations by females that encountered the males before entering the nestbox. (D) The latency of males to enter the nestbox in relation to females' wing-fluttering. Box plots show medians, first and third quartiles, outermost values with the range of 1.5 times the respective quartiles, and outliers. Observations were censored at 180 s. Data were derived from the nest visitations by males that encountered the females before entering the nestbox. See also Videos S1 and S2.

$Z = 0.84$, $p = 0.40$). Therefore, females' wing-fluttering has an independent effect on prompting males to enter the nestbox.

The wing-fluttering behavior of Japanese tits fulfills the criteria of gestures[4,6,7], as it is produced in the presence of their mate, ceases after the mate has entered the nestbox, and elicits nest entry without any direct physical contact. Notably, Japanese tits direct this behavior toward their mate, prompting them to enter the nest first, rather than fluttering their wings toward the nest entrance as if indicating its location. Thus, wing-fluttering in Japanese tits is not a deictic gesture that simply directs receivers' attention to objects, but a symbolic gesture conveying a specific message, such as a request ('after you'); this classification aligns with that of human gestures[1]. We observed a clear pattern of females exhibiting wing-fluttering more frequently than males, but its ecological significance remains an intriguing subject for future research.

While previous studies have shown that many birds use various wing displays in interactions between two individuals, such as courtship[2], our findings indicate that Japanese tits can use wing-fluttering not only as a symbolic gesture but also in a triadic context involving a signaler, a recipient, and a specific goal (i.e., nest entry) — a prominent feature of human communication[8]. In addition, Japanese tits have evolved a variety of call types and use them to indicate external referents (e.g., predator types)[9] and to create compositional messages[10]. Further comparative studies may elucidate how cognitive mechanisms underlying visual and vocal communication have co-evolved in birds, which may shed new light on theories of language evolution.

SUPPLEMENTAL INFORMATION

Supplemental information includes supplemental experimental procedures and two videos and can be found with this article online at https://doi.org/10.1016/j.cub.2024.01.030.

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AUTHOR CONTRIBUTIONS

T.N.S. designed research and wrote the paper; T.N.S. and N.S. performed research and analyzed data.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DATA AVAILABILITY

The dataset and R codes used in this study have been deposited at Mendeley Data doi: 10.17632/256z7k654k.1.

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