

Sex-biased dispersal in the Arabian babbler (*Argya squamiceps*)

 RONI OSTREIHER,*¹  ROGER MUNDY^{2,3,4,5} & AVIAD HEIFETZ⁶
¹Department of Life Science, The Open University of Israel, Raanana, Israel

²Platform Bioinformatics and Biostatistics, VetMedUni, Vienna, Austria

³Cognitive Ethology Laboratory, German Primate Centre, Leibniz Institute for Primate Research, Göttingen, Germany

⁴Department for Primate Cognition, Georg-August-University, Göttingen, Germany

⁵Leibniz ScienceCampus Primate Cognition, Göttingen, Germany

⁶Department of Management and Economics, The Open University of Israel, Raanana, Israel

Sex-biased dispersal plays a central role in shaping social structure and reproductive strategies in many bird species. In the Arabian Babbler *Argya squamiceps*, a cooperatively breeding species with pronounced male philopatry, dispersal occurs individually or in kin-based same-sex coalitions. We investigated sex differences in dispersal using 17 years of longitudinal field observations encompassing 64 dispersal events involving 156 individuals. We tested seven predictions, comparing females and males in (1) age at dispersal, (2) coalition size, (3) likelihood of dispersing alone, (4) dispersal distance, (5) duration of the transience period, (6) likelihood of encountering aggression upon joining a new group and (7) natal group size. Females dispersed at a younger age, in smaller coalitions and from smaller natal groups than males. Females also tended to disperse more often alone, and to further-away groups, though not significantly. No significant sex differences were found in transience periods, or likelihood of encountering aggression upon joining a new group. These patterns suggest that females are in more urgent need to disperse, probably because of limited reproductive opportunities within their natal groups and their subordinate position in the social hierarchy. Although we did not directly measure dispersal costs, our findings suggest that females may incur greater cumulative costs. A feedback dynamic may occur, where female-biased dispersal reinforces male philopatry, amplifying sex differences. Our results highlight the complex interplay between reproductive constraints, social organization and sex-specific dispersal strategies in cooperative breeders, and underscore the value of long-term behavioural data in understanding the evolutionary dynamics of sex-biased dispersal.

Keywords: coalition dispersal, dispersal costs, dominance hierarchy, kin cooperation, philopatry, reproductive competition.

Dispersal, defined as the movement of individuals across space with the potential for gene flow, is a fundamental evolutionary process that shapes population dynamics, genetic diversity and species persistence (Ronce 2007, Saastamoinen *et al.* 2018). Despite its potential costs, including exposure to unfamiliar environments, predation and conspecific

aggression (e.g. Maag *et al.* 2019), dispersal often enhances access to breeding opportunities and reduces the risk of inbreeding (Greenwood 1980, Johnson & Gaines 1990, Forero *et al.* 2002, Bonte *et al.* 2012).

A widespread pattern across animal taxa is that dispersal is often sex-biased (Trochet *et al.* 2016). In birds, females typically disperse more frequently than males, particularly in species with cooperative breeding systems (Greenwood 1980, Kingma *et al.* 2021). This sex bias is thought to arise from

*Corresponding author.

Email: ronio@arava.co.il

Roger Mundry and Aviad Heifetz are co-authors on this paper.

asymmetries in the costs and benefits of dispersal, which are influenced by mating systems, social structure and ecological constraints (Mabry *et al.* 2013, Trochet *et al.* 2016).

In cooperatively breeding birds, in which dominant individuals usually monopolize reproduction and subordinates assist in raising offspring, dispersal is closely linked to limited reproductive opportunities (Kingma *et al.* 2021, Ostreiher *et al.* 2022). In many such species, males are more likely to remain in their natal group, whereas females tend to disperse in search of breeding positions elsewhere (Koenig *et al.* 2000, Ridley 2012). This pattern is also evident in the Arabian Babbler *Argya squamiceps*, a cooperatively breeding passerine of arid regions, in which males are generally slightly larger and socially dominant, and females are subordinate and more prone to dispersal (Zahavi 1990). Group size ranges from 2 to 26. In addition to the dominant breeding male and female, subordinate adult males and females may also breed in some groups, depending on the social structure of the group (Zahavi 1990, Lundy *et al.* 1998, Ridley 2012, Ostreiher *et al.* 2022).

In the Arabian Babbler, sex differences emerge well before dispersal. Ridley and Huyvaert (2007) found sex-biased provisioning toward male versus female fledglings, in relation to group size and the sizes of neighbouring groups. Their findings may account for differences in early survival but cannot be extrapolated to the physical condition or competitive ability of females at the time of dispersal, approximately 2 years later.

Previous studies of Arabian Babblers indicate that dispersal may occur either individually or in kin-based same-sex coalitions, and that females are the predominantly dispersing sex (Zahavi 1989, Ridley 2012, Ostreiher *et al.* 2022). A recent theoretical model (Heifetz 2023) suggests that females may be dispersing under riskier conditions than males because of asymmetries in the ability of male and female resident group members to assist the integration of opposite-sex immigrants.

With this theoretical and empirical foundation in the background, our study investigates sex-based differences in dispersal strategies in the Arabian Babbler, using long-term observational data on individually marked birds. Specifically, we examine whether males and females differ in (1) age at dispersal, (2) size of dispersing coalitions, (3) likelihood of dispersing alone, (4) distance to the target group, (5) duration of the transience

period between leaving and joining a new group, (6) likelihood of encountering aggression upon joining and (7) size of the natal group.

Females rarely breed in their natal group – about 95% of the females that become breeders do so in non-natal groups (Zahavi 1990, Ostreiher *et al.* 2022), breeding vacancies are limited (Zahavi 1989, 1990), and females cooperate less with other females in breeding than males do with other males (e.g. dominant females typically do not tolerate other females laying in the single communal nest, whereas dominant males are more tolerant of subordinate males copulating with the breeding females (Ostreiher *et al.* 2022)). For this reason, we predicted that, compared with males, females would: (1) disperse at a younger age, (2) disperse in smaller coalitions, (3) more often disperse alone, (4) disperse to more distant groups (i.e. non-adjacent to the natal group), (5) experience longer transience periods between departure and successful integration, (6) face augmented aggression upon joining a new group and (7) disperse from smaller natal groups. Prediction (7) is based on the notion that competition over food is more intense in large groups than in small ones (Anava *et al.* 2001). Females are subordinate to all adult males (Zahavi 1990) and may experience higher foraging success in smaller groups. Dispersal from a small group therefore incurs higher opportunity costs (Bonte *et al.* 2012) than dispersal from a large group. We predicted that, in search of breeding opportunities, females would bear this higher opportunity cost and disperse from smaller groups more often than males. By testing these predictions, we aim to clarify how sex-based differences manifest in the dispersal behaviour of Arabian Babblers and to contribute to a broader understanding of dispersal strategies in cooperatively breeding species.

METHODS

Field methods

This project was conducted from January 1991 to December 2008 in and around the Shezaf Nature Reserve, located approximately 30 km south of the Dead Sea in southeastern Israel. In Arabian Babblers, the adult male's eye ring is light yellow and the adult female's eye ring is dark brown. The difference becomes clear at the age of 8–9 months. Each individual bird in the research area was

ringed with a unique combination of four coloured rings as a 10-day-old nestling. The Arabian Babblers in the research area were habituated to the presence of human observers, allowing researchers to document their complex social behaviour from close distances (Zahavi 1989, 1990). During the data collection period for this study, each group was visited one to three times per week to document group composition. The hatching date of each individual in the study population was known (± 2 days), enabling us to determine their ages at the time of departure from their natal groups.

During the study period (1991–2008), the research area included approximately 40 territorial groups, each consisting of 2–26 individuals of both sexes and all ages. Over this time, 159 males successfully became the dominant male in a group. Of these, 97 (61%) achieved dominance within their natal group, and 62 (39%) became dominant in a different group after successful dispersal. In contrast, 125 females attained the position of dominant female in a group. Of these, eight (6.4%) achieved dominance in their natal group after the arrival of new males, while 117 (93.6%) became dominant in a different group following successful dispersal. These findings confirm the conclusion of Zahavi (1990) that females are the predominant dispersing sex in this species.

Since the beginning of the Arabian Babbler research project in 1971, we have documented the results of 378 dispersal events. As Zahavi already noted (Zahavi 1990), most of them (298; 79%) were performed by unisex subgroups of subordinate young adults that could not breed within their natal groups. In 73 dispersal events, we happened to be present when one or more individuals, either males or females, left their group. We can confirm that none of these individuals were evicted, nor was there any aggression associated with their departures. In all the cases, we followed the dispersers until they went to roost, and on the following days, we tracked them from first light until nightfall, documenting whether they successfully joined a new group or failed to do so and the group broke up. In nine cases, we lost track of the dispersers before determining whether they succeeded or failed in their dispersal attempts. In cases where individuals failed to join a new group, we documented their continued movements or disappearance whenever possible, but it should be noted that some failed dispersal attempts may not have been detected or fully tracked.

The meeting between dispersers and a group always occurred within the group's territory, where the dispersers were intruders. Of 64 dispersal events, in four cases residents discovered the dispersers, attacked them and chased them away, resulting in failed integration. In the remaining 60 successful integrations, first contact was always initiated by the dispersers, after they had remained in the group's territory for at least 5 h; in four cases, they waited up to 2.5 days before making any vocal or physical contact.

In 23 cases (38.3% of the 60 successful integrations), dispersers joined without aggression, usually following the disappearance of the resident dominant of the same sex. In 19 of these cases, no adult of the same sex as the disperser was present. Dispersers typically approached slowly toward a resident, which in reaction stopped foraging and stood motionless, after which the newcomer began to preen the resident. This could also be initiated simultaneously by another disperser with another resident. The allopreening often developed into mutual allopreening, sometimes involving several residents in sequence. The process usually lasted less than 10 min, after which dispersers foraged together with residents without apparent tension.

In 34 cases, dispersers entered a roost tree when it was already completely dark, after residents had settled for the night, either in the same tree or in an adjacent one. Interactions began the following morning, well before sunrise. In 24 cases (out of 37 aggressive successful integrations), residents immediately attacked the newcomers as they descended from the roost tree. The dispersers initially retreated but repeatedly returned, and in most cases the roles eventually reversed: a disperser attacked a resident and displaced the dominant individual of the same sex. In many events, dispersers did not initiate aggression but approached residents cautiously, retreated when attacked and tried again minutes later. In most cases, they reacted aggressively only at a very late stage of the interactions. These encounters often lasted several hours, sometimes the entire day, and in two cases continued for 2 days.

With five exceptions, dispersers did not seem to act as a coordinated unit. Each individual acted separately, though often simultaneously. Each attempted to approach residents, usually without aggression, and either retreated or responded aggressively, depending on the resident's reaction. Exceptions occurred in five cases (all male events),

when two to four dispersing males, usually brothers, jointly attacked the resident dominant male, chased him away from the group and the territory, and displaced him. These coalitionary takeovers were completed within less than an hour.

Aggressive interactions happened very quickly, over large distances, with several dyads acting in parallel and with opponents frequently switching. As a result, and because we did not use video cameras, we were usually unable to determine the direction, intensity or duration of aggressive interactions. We were therefore unable to quantify these parameters. Our data only indicate whether an individual was involved in aggressive interactions during the process of integrating into a new group.

For the current study, we focused on 64 dispersal events involving 156 participants, for which we were able to record the following parameters: the size and composition of the group of origin, the age (± 2 days) of each participant, whether there was a common border between the original group and the target group, transience time (defined as the duration from leaving the original group to joining the new group, as per Clobert *et al.* (2009)), and whether joining the target group involved fights with resident members.

In total, we spent 325 full days in the field observing dispersers from when they left the natal group to the conclusion of the dispersal event (either successfully joining a new group or failing to do so). We were able to determine the outcome of the dispersal for each of the 156 participants, and no experimental manipulations were used.

One limitation of our study is that the dispersal events we documented may not represent all dispersal attempts in the study population. It is possible that we missed unsuccessful dispersal events, particularly those involving single individuals. However, without direct observations, it is impossible to distinguish such events from evictions or predation, so we are unable to quantify how common they were within the study population. Similar challenges have been reported in studies of other species (Bowen *et al.* 1989, Koenig *et al.* 2000).

Statistical analyses

To test our predictions and conduct the exploratory analysis, we fitted a total of seven mixed

models; one was a Linear Mixed Model (LMM), and the others were Generalized Linear Mixed Models (GLMMs) (Baayen 2008). In all models, sex was included as the only fixed effect, and both group of origin and target group were included as random intercept effects. The models only differed in the response variable, the sample size, as well as their error structure and link function (McCullagh & Nelder 1989). Furthermore, in case the analysed data comprised multiple data points per dispersal event, we included an additional random intercepts effect for the identity of the dispersal event. Further details about the seven models fitted for this study can be found in Table 1.

The unit of analysis differed between models. Model 1 (response variable: age at dispersal) was fitted with individual-level data in which each data point represents a single dispersing individual. Models 2–7, which examined characteristics of the dispersal event such as coalition size or transience time, were analysed at the dispersal-event level, with each data point representing a single dispersal event. For this reason, the sample size is larger for model 1 than for the other models. In the case of models 2, 3 and 7 – with the response variables being coalition size, whether the individual dispersed alone and the size of the group of origin, respectively – the response could be determined, irrespective of whether the dispersal attempt was successful or not. Hence, the datasets analysed with these models comprised all 64 dispersal events. In the case of the four unsuccessful attempts, we assigned each attempt a unique dummy target group. Models 4, 5 and 6 – with the response variables being whether the dispersal was to a non-neighbouring group, the transience time and whether the dispersal involved aggression, respectively – the response could obviously only be determined for the 60 successful dispersal events.

In order to meet the assumptions of model 1, namely normally distributed and homogeneous residuals (assessed by visual inspection of a *qq*-plot of residuals and residuals plotted against fitted values), we log-transformed age in model 1 (base *e*). Into this model we included an additional random intercept effect for the ID of the event because the dataset analysed frequently comprised several individuals per dispersal event. Indications for over-dispersion were not found in any of the models with a count response (models 2, 5 and 7; Table 1).

Table 1. Specifications of the models fitted.

Model number	Response	Error structure, link function	Total sample size	Number of levels per random effect	Remarks
1	Age at dispersal (days)	Gaussian, identity	156	64 dispersal events, 47 natal groups, 41 target groups	
2	Coalition size	Poisson error, log	64	47 natal groups, 41 target groups	Dispersion parameter: 0.42
3	Probability to disperse alone	Binomial error, logit	64	47 natal groups, 41 target groups	1 dispersal by a single individual
4	Probability to disperse into a non-neighbouring group	Binomial error, logit	60	45 natal groups, 37 target groups	33 dispersals into non-neighbouring groups
5	Time lag between leaving and joining (days)	Negative binomial, log	60	45 natal groups, 37 target groups	Dispersion parameter: 0.99
6	Probability of joining the target group involved aggression	Binomial error, logit	60	45 natal groups, 37 target groups	38 joining events involved aggression
7	Size of the group left	Poisson error	64	47 natal groups, 41 target groups	Dispersion parameter: 0.80

The column headed 'Remarks' indicates the dispersion parameter where relevant (Poisson and negative binomial models), and for binomial models we indicate the number of positive outcomes.

Regarding model 5, with which we analysed the time lag between leaving and joining, we are aware that a negative binomial error distribution is not fully appropriate for such a response variable. This is because the probability to join a new group might not be constant over the entire period between leaving the old group and joining the new group. However, a Gaussian error distribution was not possible because of highly heteroscedastic residuals, and using a gamma error distribution led to a highly over-dispersed model. Hence, the results of this model should be treated cautiously.

We fitted all models in R (version 4.5.1; R Core Team 2025), using the functions `lmer` (model 1, the LMM) or `glmer` (models 2, 3, 4, 6, 7) of the package `lme4` (version 1.1-37; Bates *et al.* 2015) or the function `glmmTMB` of the equally named package (version 1.1.11; Brooks *et al.* 2017) for model 5. In all models, we dummy coded sex with females being the reference level. For all models, we estimated model stability (i.e. how sensitive model results are to the presence or absence of, for example, individual, groups of origin or individual target groups) by dropping the individual levels of the random effects factors (i.e. individual groups of origin, individual target groups and also individual events in the case of model 1) one at a time and fitting the full model to each of the obtained subset datasets (Nieuwenhuis

et al. 2012). We then determined the range of estimates obtained with those the model fitted to the full dataset. With the exception of model 3, all models were of acceptable excellent stability (see Table 2). We determined 95% confidence intervals of the estimated coefficients and fitted values by means of a parametric bootstrap (function `bootMer` of the package `lme4`). In case of the LMM (model 1) we determined the significance of the factor sex by means of the Satterthwaite approximation (Luke 2017), which we obtained by fitting an additional model based on restricted maximum likelihood and using the function `lmer` of the package `lmerTest` (version 3.1-3; Kuznetsova *et al.* 2017). For the other models, we determined the significance of the factor sex by dropping it from the model and comparing the fit of the resulting reduced model with that of the full model using a likelihood ratio test (R function `drop1`; Dobson 2002).

RESULTS

Overall, out of the 64 dispersal events, in 43 events the dispersers were females, in which there were a total of 91 dispersing individuals, whereas in 21 events the dispersers were males, in which there were overall 65 dispersing individuals. The results of the seven models are presented in Table 2.

Age on the day of the dispersal event (prediction 1)

Model 1 revealed that females dispersed at a younger age than males (Table 2; Fig. 1a). The youngest individual that dispersed was 325 days old, and the oldest was 2825 days old, with an average of 938 ± 383 (arithmetic mean $\pm$ sd) days. Females dispersed at a median age of 755 days (interquartile range (IQR) 686.5–918 days), and males dispersed at a median age of 980 days (IQR 790–1220 days).

Size of the dispersing coalition (prediction 2)

Most dispersal events involved two to four dispersers (i.e. same-sex adults without breeding potential in the group). Median male coalition size was 3 (IQR 3–4) individuals, and median female coalition size was 2 (IQR 1–3) individuals. Females dispersed in smaller coalitions than males (model 2; Table 2; Fig. 1b).

Dispersing alone (prediction 3)

Females tended to disperse alone more frequently than males (Model 3; Table 2). Of the 43 dispersal

events involving females, 12 (27.9%) were carried out by a single female that dispersed while other non-breeding females in her group remained. Of these 12 females, two disappeared after arriving at the target group and before integrating into it. Of the remaining 10 females that successfully joined a target group, nine eventually attained breeding status. In contrast, of the 21 dispersal events involving males, only two (9.5%) involved a single male dispersing while other non-breeding males remained in the group. Both males succeeded in becoming breeders in their target groups. Of the 14 individuals (females and males) that dispersed alone, five moved to a neighbouring group (four became breeders and one disappeared), and nine moved to a group that did not share a border with their original group.

Probability to disperse into a non-neighbouring group (prediction 4)

Sixty successful dispersal events were categorized according to whether there was a common border between the original group and the target group. Out of 40 dispersal events performed by females, 15 (37.5%) moved to a neighbour group with a common border, and 25 (62.5%) moved to a group without a common border. Out of 20

Table 2. Results of the models fitted with the seven response variables (age at dispersal, coalition size, probability to disperse alone, probability to disperse to a non-neighbouring group, time lag between leaving the natal group and joining a new group, probability of aggression when entering the new group, and natal group size).

Response (model)	Term	Est.	se	CL _{lower}	CL _{upper}	χ^2 or t	df	P	Min	Max
Dispersal age (model 1)	icpt	6.673	0.039	6.603	6.745				6.658	6.694
	sex	0.243	0.057	0.130	0.356	4.200	60.89	<0.001	0.211	0.268
Coalition size (model 2)	icpt	0.750	0.105	0.525	0.928				0.717	0.775
	sex	0.380	0.162	0.061	0.675	5.337	1	0.021	0.349	0.419
Dispersing alone (model 3)	icpt	-11.544	3.152	-23.523	-8.407				-17.587	-1.444
	sex	-17.352	8.200	-28.745	2.382	3.710	1	0.054	-19.206	-2.235
Probability to disperse to non-neighbouring group (model 4)	icpt	0.533	0.355	-0.102	2.440				0.406	0.691
	sex	-0.942	0.595	-3.857	0.201	2.610	1	0.106	-1.218	-0.712
Leave join lag (model 5)	icpt	1.775	0.304	0.765	2.230				1.529	1.822
	sex	-0.745	0.535	-1.979	0.327	1.749	1	0.186	-1.355	-0.500
Joining style (peaceful vs. violently; model 6)	icpt	0.552	0.372	-0.101	10.192				0.434	0.668
	sex	0.142	0.615	-1.255	1.912	0.054	1	0.816	-0.024	0.361
Left group size (model 7)	icpt	2.044	0.055	1.932	2.148				2.023	2.055
	sex	0.215	0.089	0.015	0.390	5.669	1	0.017	0.182	0.248

Indicated are estimates (Est.), together with their standard errors (se), 95% confidence limits (CL), significance tests and the range of estimates (minimum (Min), maximum (Max)) obtained when dropping the individual levels of the random effects one at a time. The significance test of model 1 was a t -test with degrees of freedom based on the Satterthwaite approximation, while in all other models it was a likelihood ratio test comparing the model including sex with one which lacked it. Sex was dummy coded ($F = 0$, $M = 1$), and hence the estimates inform about how much males differed from females. 'icpt' refers to model intercept.

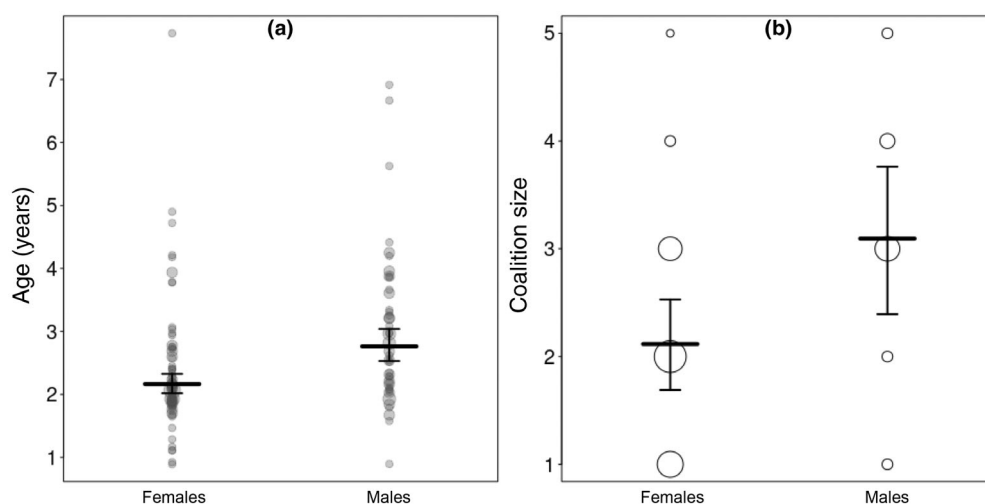


Figure 1. Age at dispersal (a, model 1) and coalition size (b, model 2), separately for females and males. The dots show the raw data, whereby the area of the dots in (a) and (b) depicts the frequency of occurrence of a given observation per sex (range: 1–5 in (a) and 1–18 in (b)), and in (a) the dots are additionally semi-transparent to better visualize the points where there are concentrations of overlapping data points. Horizontal lines with vertical error bars depict the fitted model's estimate and its 95% confidence interval, respectively.

dispersal events performed by males, 12 (60%) moved to a neighbour group with a common border, and 8 (40%) moved to a group without a common border. Although the tendencies are opposite, the differences between the sexes were not statistically significant (model 4, Table 2).

Transience time (time lag between leaving and joining) (prediction 5)

The median transience time was 1 (IQR 0–6) day per event. The shortest dispersal event concluded on the same day as departure (28 cases, 47%, were 1-day events), whereas the longest lasted 56 days (one case involving a lone female). Most dispersal events (49 out of 60, 82%) were completed in at most 7 days. Transience time for males was shorter than for females, though not significantly so (model 5; Fig. 2a; Table 2). Out of 40 successful dispersal events involving females, 14 (35%) were concluded on the day of leaving the group of origin. Out of 20 successful dispersal events involving males, 14 (70%) were concluded on the day of leaving the group of origin. The time lag between leaving and joining ranged between 0 and 56 days for females, with a median of 2 (IQR 0–6) days. For males it ranged between 0 and 24 days, with a median of 0 (IQR 0–1.75) days.

In 11 cases (out of 15) in which dispersing females moved to a neighbouring group with a common border, transience time was 0 days. In the other four it was 1, 1, 2 and 3 days. In the 25 events in which females dispersed to a further-away group (without a common border), three were concluded on the same day, with a median of 6 (IQR 2–12) days. In 11 cases (out of 12) in which dispersing males moved to a neighbouring group with a common border, joining took place on the same day (time gap of 0 days), and in the remaining case it was 1 day. In the eight events in which males dispersed to a further-away group (without a common border), three were concluded on the same day, with a median of 4 (IQR 0–11.25) days.

Entering the target group with or without aggressive interactions (prediction 6)

No difference was found between females and males regarding the way they joined the target group – joining without aggressive objection into a breeding vacancy or fighting against certain group members and chasing them away (Table 2). Out of 40 dispersal events, in 16 cases (40%) females joined without aggressive interactions and in 24 events (60%) they joined aggressively. Out of 20

dispersal events, in seven (35%) males joined without aggressive interactions and in 13 events (65%) they joined aggressively.

Natal group size (prediction 7)

Females dispersed from significantly smaller groups than males (model 7; Table 2). Females dispersed from groups whose size was on average 7.7 ± 2.4 sd individuals (before leaving) and males dispersed from groups whose size was 9.6 ± 2.8 sd (Fig. 2b).

DISCUSSION

Our study provides detailed insights into sex differences in dispersal behaviour in Arabian Babblers. Using long-term observational data, we found that females and males differed in several key aspects of dispersal, including age at dispersal, coalition size, likelihood of dispersing alone and dispersal distance. Below, we interpret these findings in light of current theory and previous empirical research.

Females dispersed at a younger age than males. This finding supports earlier suggestions that subordinate females have limited prospects for breeding within their natal group and therefore disperse earlier in pursuit of alternative opportunities (Zahavi 1989, 1990, Ridley 2012). In contrast,

subordinate males may benefit from remaining in their natal group while awaiting potential breeding vacancies (Zahavi 1990, Ridley 2003, Ostreiher *et al.* 2022). These differences in expected reproductive returns probably underlie the observed sex-based asymmetry in dispersal timing.

Males were more likely to disperse in larger coalitions, whereas females tended to more often disperse alone. This pattern is consistent with previous findings in cooperatively breeding birds (Koenig *et al.* 2000) and may reflect the underlying social and ecological dynamics, such as male–male alliances and the benefits of coalition-based integration, as shown by Schoof *et al.* (2009) and Ridley (2012). We did not directly test whether coalition size increases the likelihood of successful integration, but the prevalence of male coalitions suggests that social support may facilitate entry into new groups. The tendency for females to disperse alone, despite the apparent benefits of coalitionary dispersal, may reflect sex-specific strategies. For example, females may be more readily accepted into new groups because of their reproductive value or lower threat to existing dominance hierarchies. In addition, female solitary dispersal may help avoid future competition among reproductive females, which is particularly relevant in this species in which the cooperative efforts of the entire group are required to raise four offspring laid by a single female in a

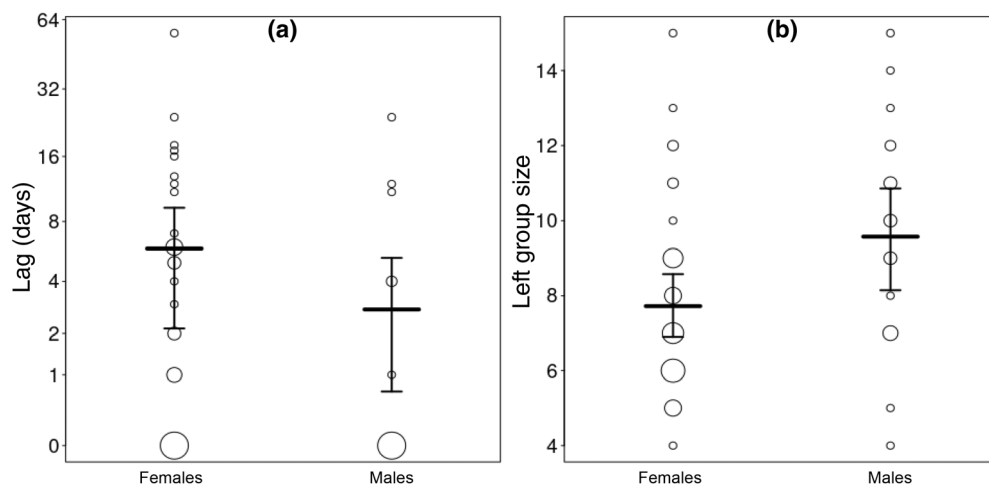


Figure 2. Time lag between leaving the group of origin and joining a new group (a, model 5) and the size of the group of origin before leaving (b, model 7), separately for females and males. The dots show the raw data whereby the area of the dots depicts the frequency of occurrence of a given observation per sex (range: 1–14). Horizontal lines with vertical error bars depict the fitted model's estimate and its 95% confidence limit, respectively.

communal nest (Ostreiher 1997). Alternatively, solitary dispersal by females may indicate greater urgency or strategic flexibility in accessing limited breeding opportunities. However, this strategy probably incurs higher costs, as female dispersers tended to move farther and for longer durations (though not significantly so).

Females dispersed over longer distances than males albeit not statistically significantly. Still, in 63% of the female dispersals, but only 40% of the male dispersals, the dispersing birds joined a non-neighbouring group. This finding is consistent with the general pattern of female-biased dispersal in birds (Greenwood 1980, Mabry *et al.* 2013). Longer dispersal distances, along with solitary dispersal, may help females avoid kin competition and increase their chances of joining unrelated groups with breeding vacancies. In Southern Pied Babblers *Turdoides bicolor*, genetic analysis showed that dispersers move beyond the probable spatial range of close kin, effectively reducing inbreeding and kin competition (Nelson-Flower *et al.* 2012). In Superb Starlings *Lamprolornis superbus*, immigrant females almost exclusively join non-kin groups, suggesting that long-distance dispersal facilitates entry into unrelated social units with breeding opportunities (Shah & Rubenstein 2023). Theoretical models emphasize that both kin competition avoidance and limited local breeding spots can drive sex-biased dispersal, generally favouring longer female movements (Li & Kokko 2019). In contrast, males may benefit from staying near their natal territory because of their familiarity with it or the possibility of inheriting a local breeding position. Male Acorn Woodpeckers *Melanerpes formicivorus* that remained in their natal territories were much more likely to become breeders than those that dispersed, suggesting that philopatry itself may enhance reproductive prospects (Koenig *et al.* 2023). Consistent with this, comparative data from a multi-species analysis of cooperatively breeding birds demonstrated that territory inheritance prospects strongly predict helping behaviour and reproductive success, supporting the hypothesis that staying in the natal territory offers significant direct benefits to males (Kingma 2017). Similarly, in the cooperatively breeding cichlid fish *Neolamprologus pulcher*, individuals that remained philopatric achieved higher fitness than dispersers, reinforcing the potential advantages of remaining in or close to the natal group (Jungwirth *et al.* 2023).

We did not find a significant difference between sexes with regard to the time elapsed between leaving the group of origin and joining a new group. Still, the estimated transience time for females (5.9 days) was more than twice that of males (2.8 days). This may result from their higher likelihood of dispersing alone or covering longer distances, both of which can hinder rapid integration into a new group. Although we did not directly quantify the immediate costs associated with the dispersal event, this result suggests sex-based differences in the dynamics and potential costs of dispersal.

Contrary to our prediction, we found no significant difference between the sexes in the likelihood of experiencing aggression upon joining a new group. As explained in the Methods, because aggressive interactions occur very quickly, often over long distances, and with frequent changes in direction (as attacker and recipient swap roles), we were usually unable to determine their direction, intensity and duration. Our data only reveal whether an individual was involved in aggressive interactions in the course of integrating into a new group. Previous studies demonstrated that cooperatively breeding residents prevented dispersers aggressively from joining their groups in Siberian Jays *Perisoreus infaustus* (Griesser *et al.* 2008), Tibetan Ground Tits *Pseudopodoces humilis* (Guo *et al.* 2020) and cichlid fish *Neolamprologus pulcher* (Zöttl *et al.* 2013). Our findings may indicate that resistance to immigrants is not sex-specific, or that other factors, such as competition for breeding positions, dominance status, group composition or seasonal timing, play a more decisive role than sex per se. However, integration into a new group involves a range of behaviours. Further studies should focus on subtle affiliative interactions between immigrants and residents, on their transition and escalation from friendly to aggressive behaviour, and on the social relationships among residents before immigration.

On average, females dispersed from smaller natal groups than males. Males, but not females, sometimes occupy neighbouring territories with the help of their parental group (Zahavi 1989). Females, which tend to disperse over longer distances, may not benefit from such assistance. Males leaving larger groups may have an advantage, as those groups are better able to provide support. In addition, smaller groups may offer better foraging conditions, particularly for subordinate

females, because of reduced competition over food (Heifetz 2023). Hence, dispersal from small groups probably reflects a strategic response by females to reproductive constraints in their natal groups, despite the short-run benefits of staying.

In summary, more females disperse than males and, compared with males, females dispersed at a younger age, from smaller natal groups, more frequently alone or in smaller coalitions. Females also tended to disperse over longer distances, and the duration of their dispersal was longer (although these were not statistically significant). These traits are not independent. Dispersing at a younger age means that there are fewer younger sisters that could potentially join the dispersal. As males tend to disperse to neighbouring groups with a shared border, and as Arabian Babblers do not copulate with individuals that lived in their group during their upbringing (Zahavi 1990), females might have to disperse farther, which then also might take more time. Additionally, small groups produce fewer offspring than large groups (Zahavi 1989, Zahavi & Zahavi 1997), which may be another reason why females, which tended to disperse from smaller groups, also form smaller dispersing coalitions.

The tendency of females to disperse more frequently than males may also discourage mature, non-breeding males from dispersing, as they may benefit from remaining and eventually breeding with incoming females. This dynamic could create a reinforcing feedback loop that amplifies sex differences in dispersal strategies and deepens reproductive asymmetry between the sexes.

Importantly, these insights were made possible by a long-term dataset tracking individual dispersal events over many years. The richness and continuity of such data allow for detecting subtle sex differences, rare dispersal strategies, and occasional structural changes in group social and breeding organization, such as transitions from a single breeding pair to multiple breeders within the same group, that might be overlooked in shorter studies. Following Clutton-Brock and Sheldon (2010), we also realized that long-term behavioural studies are crucial for understanding the evolutionary dynamics of sex-biased dispersal and the social systems in which they occur.

Together, our findings support the view that dispersal strategies in Arabian Babblers are sex-biased and shaped by reproductive constraints, ecological factors and social dynamics. Although we did not directly measure dispersal costs such as

survival, changes in body condition or reproductive success, our results raise the possibility that females may incur higher cumulative costs associated with dispersal. Future research incorporating direct measures of these costs will be essential to test this hypothesis.

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AUTHOR CONTRIBUTIONS

Roni Ostreiher: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review and editing; project administration; resources. **Roger Mundry:** Conceptualization; writing – original draft; methodology; validation; visualization; writing – review and editing; software; formal analysis; data curation. **Aviad Heifetz:** Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review and editing; resources.

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CONFLICT OF INTEREST

The authors declare no competing interests.

ETHICAL NOTE

The study was based on observations only, and no experimental manipulations were carried out. The research adhered to the ASAB/ABS Guidelines for the Use of Animals in Research and the requirements of the Nature Reserve Authority in Israel (Permissions No. 32915 and 41723).

Data Availability Statement

The data analysed in this study are available as Data S1.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Supplementary file for sex-biased dispersal in the Arabian Babbler.