Component, Group and demographic Allee effects in a cooperatively breeding bird species, the Arabian babbler (*turdoides squamiceps*)

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This study is a result of a unique data analysis, covering more than 35 years of comprehensive, long term data collected on the cooperatively breeding Arabian babbler. This study joins recent papers on cooperatively breeding species in describing component and group Allee effects, but furthermore, it is the first to discover a demographic Allee effect in any cooperatively breeding species. We believe that these findings will provide a major contribution to an overall understanding of the factors influencing population dynamics in cooperative breeders

Declaration of authorship

Author Contributions: OK designed the analysis and analyzed the data with the supervision of ARR. OK & ARR wrote the manuscript. The authors declare that they have no conflict of interests.

26 **Abstract**

27 In population dynamics, inverse density dependence can be manifested by individual fitness
28 traits (component Allee effects), and population-level traits (demographic Allee effects).
29 Cooperatively breeding species are an excellent model for investigating the relative
30 importance of Allee effects, because there is a disproportionately larger benefit to an
31 individual of being part of a large group. As a consequence larger groups have greater
32 performance than small groups, known as the group Allee effect. Although small populations
33 of cooperative breeders may be prone to all levels of Allee effects, empirical evidence for the
34 existence of a demographic Allee effects are scarce. In order to determine the extent to which
35 Allee effects are present in a cooperatively breeding species, we used a comprehensive 35-
36 year life history database for cooperatively breeding Arabian babblers (*Turdoides*
37 *squamiceps*). Firstly, we confirmed the existence of a component Allee effect by showing
38 that breeding individuals in large groups receive greater benefits than those in small groups;
39 second, we confirmed the existence of group Allee effect by showing that larger groups
40 survive longer. And thirdly, we identified a demographic Allee effect by showing that per
41 capita population growth rate is positively affected by population density. Finally, we found
42 that emigration and immigration rates, although dependent on group size, do not buffer
43 against component and group-level Allee effects becoming a demographic Allee effect. Our
44 finding of the existence of all three levels of Allee effects in a cooperative breeder, may have
45 important implications for future research and conservation decisions.

46 **Keywords:** Allee effect, Arabian babblers, cooperation, density dependence, group size
47 population dynamics.

48 **Introduction**

49 A positive increase in individual fitness with population size or density is known as *inverse*
50 *density dependence*, or an Allee effect (named after the pioneering American ecologist
51 Warder Clyde Allee who was the first to describe them (Allee 1931). According to this effect,
52 more individuals in a population will result in higher fitness per individual, until negative
53 density dependence effects (such as competition over reproduction or resources) occurs at
54 high population density or size. An Allee effect could influence small populations by several
55 mechanisms (reviewed by Stephens et al. 1999; Courchamp et al. 1999a; Stephens and
56 Sutherland 1999; Courchamp et al. 2008). These mechanisms include limitation in the ability
57 to find mates (Wells et al. 1998), inbreeding depression (Willi et al. 2005), higher per capita
58 risk of predation (Bourbeau-Lemieux et al. 2011) and higher vulnerability to both
59 environmental stochasticity and genetic drift (Willi et al. 2005). The relative strength of the
60 Allee effects influencing individual fitness components will determine the overall influence
61 of Allee effects on the population (Stephens et al. 1999). Therefore, Stephens and Sutherland
62 (1999) suggested that in order to better study Allee effects in animal populations, it would be
63 useful to distinguish between component Allee effects, which are manifested by individual
64 fitness traits (increased individual fitness with population size), and demographic Allee
65 effects, which are manifested by the level of total fitness represented by per capita population
66 growth rate in relation to population size.

67 Although the presence of component Allee effects has previously been demonstrated in
68 several species of both social and non-social animals (reviewed by Kramer et al. 2009), there
69 has thus far been very little evidence for demographic Allee effects in any species of
70 vertebrate (Angulo et al. 2007; Gregory et al. 2010). One explanation for the scarcity of
71 evidence may be because Allee effects in one component of fitness may be offset by an
72 increase in other components of fitness, thus creating a weak demographic Allee effect that

doesn't reach the population threshold (Berec et al. 2007; Angulo et al. 2007; Gregory et al. 2010). Although social species are more sensitive than non-social species to the existence of an Allee effect (Courchamp et al. 1999b; Somers et al. 2008), evidence for a demographic Allee effect in these species does not exist and the mechanisms that prevent component Allee effect from becoming demographic are not yet clear.

Cooperatively breeding species, where more than two individuals help care for the young raised from a single brood (reviewed in Koenig and Dickinson 2004; Cockburn 2013; Riehl 2013) may be particularly sensitive to Allee effects (Courchamp et al. 1999b; Somers et al. 2008). This is because in cooperatively breeding species, and particularly in obligate cooperative breeders, individual survival and reproduction are strongly affected by group size, with larger groups providing increased benefits to individuals such as lower costs of parental care (Ridley and Raihani 2007; Russell et al. 2007; Cockburn et al. 2008; Meade et al. 2010), increased predator vigilance (Beauchamp 2008; Bell et al. 2009; Sorato et al. 2012; Ridley et al. 2013), better access to food resources (Kokko et al. 2001) and better access to dispersal opportunities (Ridley 2012). A group that decreases in size may therefore be more likely to suffer a further decrease, or even become extinct (Courchamp et al. 1999 b; Angulo et al. 2013). Angulo et al. (2013) suggested that since individual fitness is more dependent on within-group dynamics than overall population size, the group should be considered an independent level of organization, what has been called the 'group Allee effect' - i.e. when the performance of a group (group growth, group survival) increases with the size of the group. Group Allee effects should be considered in order to better understand inverse density dependence in cooperative breeders. Courchamp et al. (1999 b) have suggested that high extinction rates for small cooperatively breeding groups are due to the existence of an Allee threshold of group size. In addition, Bateman et al.(2011) proposed that in cooperative breeders, component Allee effects may not translate to a demographic Allee effect because

group growth rates are asynchronous with population growth rates, resulting in different factors influencing group and population-level dynamics.

In this paper we use an extensive long-term dataset covering 35 years of continuous research on cooperatively breeding Arabian babbler groups (*Turdoides squamiceps*) to test for evidence of component, group and demographic Allee effects. We aim to (1) investigate the existence of component Allee effects by testing whether the average annual reproductive rate of breeding individuals are influenced by group size, population density (number of individuals /km²) or group density (number of groups/km²), (2) determine the existence of a group Allee effect by testing whether group dynamics (i.e. group persistence probability) are affected by group size, population or group density, and (3) test for evidence of a demographic Allee effect by examining whether per capita population growth rate is affected by population or group density. If inverse density dependence does occur in the population, we expect that reproductive success, group persistence probability and per capita population growth rate should increase with either group or population size or density. In order to better understand the mechanisms that regulate the presence of Allee effects in our study population, we examine immigration and emigration rates between groups in order to determine whether inter-group interactions play a role in preventing component and group Allee effects from turning into demographic Allee effects (as suggested by Bateman et al. 2012). By investigating all of these aspects we aim to create a comprehensive overview of the factors influencing the existence of different levels of Allee effects in a cooperatively breeding species.

Materials and Methods

Study site and population

Our study was conducted in the Negev desert, south-east Israel (30°48'N, 35°13'E), at the Shezaf Nature Reserve, a 40 km² protected wildlife area in the Arava region surrounded by approximately 20 km² of farmland. The habitat is defined as hyper-arid desert (rainfall <50mm per annum, UNESCO 1977). A long-term research project on the ecology of the cooperatively breeding Arabian Babbler has been continuously conducted in the area since 1971 by Prof Amotz Zahavi (Zahavi 1989; Zahavi 1990; Zahavi and Zahavi 1997). Each individual in the population is ringed with a unique combination of one metal and three coloured rings, and all individuals are habituated to human presence (for a description of habituation, see Zahavi and Zahavi 1997; Ridley 2007; Ridley and Raihani 2007), allowing close-range observations.

Arabian babblers are a group-territorial, cooperatively breeding bird species with age-related linear dominance hierarchies within each sex class (Zahavi 1989; Zahavi 1990). Each group usually contains only one dominant breeding pair, although subordinate individuals that are unrelated to the dominant pair may gain reproductive success on rare occasions (less than 5% of breeding attempts, Lundy et al. 1998). Groups differ in their size (ranging from 3 -17 adults) and are highly territorial year-round. The breeding season usually starts around the end of February and continues until July (Zahavi 1989; Zahavi 1990). Only one nest is active at a time, and usually all adult group members help in raising young (Ridley 2007). Juveniles are considered adults when they reach 12 months old. At about this age it is possible to discriminate between the sexes through sexual dimorphism in beak shape and sexual dichromatism in eye colour (Ostreiher 1999; Ridley 2007).

Data collection

We used data that was continuously collected on cooperative groups of Arabian babblers between 1978 and 2013. During this period, all groups were visited at least once every month

outside the breeding season, and at least once a week during the breeding season to monitor group size and composition. We extracted and cross-examined the data from different sources (a Microsoft Access database, field notes and large cardboard datasheets). This resulted in a dataset comprising 79 different groups and totalling 908 group-years. For the analysis of group persistence and annual reproductive rate we only used groups that had a complete group history in all three sources, resulting in a dataset comprising 43 groups. We defined annual group size as the number of individuals in each group at the last observation in December of each year (i.e. before the breeding season): we chose this date because breeding activity is typically absent in December (Zahavi 1989; Zahavi 1990), but the juveniles from the previous breeding season have reached nutritional independence and participate in all group activities. To measure group and population density we calculated the geographical area that the entire study population occupied each year (defined as the area in which established groups were present and regularly observed), using Google Earth version 7.1.2 and GEpath 1.4.6). We determined group density by dividing the number of groups by the total area, and population density by dividing the number of individuals by the total area.

Population and group demographic trends over time

To assess the population and group demographics over the past 35 years (1978-2013), we plotted individual and group variables (annual reproductive rate, average group size) and population variables (number of groups per km², and per capita population growth rate) over time.

Testing for component, group and demographic Allee effects

A component Allee effect may exist if the survival of the individual and/or its annual reproductive rate is positively affected by group size or population size or density. In order to determine the presence of a component Allee effect in this study we measured the annual

reproductive rate for each group (as a measure of annual reproductive rate for the breeding pair), defined as the number of nestlings that fledged from the group's nests each year.

As for a component Allee effect, a group Allee effect may exist if group demographics (in this case, probability of group persistence per annum) are positively affected by group size, population size or population density. Each group was assigned a 0 or 1 for each year of observation, where 0 = extinct, 1 = survived. A group that went extinct could not reappear in the database as extant the following year. We defined a group as extinct when all individuals had dispersed or disappeared and repeated investigations found no further evidence of the group. All of the groups in our study population were observed at least once a month, and all territories are located in places that are still monitored to this day. Thus, we do not think it is likely that we misclassified some groups as extinct that were in fact still extant but had changed territory slightly. Arabian babblers are both poor fliers and highly territorial (Zahavi & Zahavi 1997). When a group goes missing, we search extensively for them well beyond their territory borders on repeated occasions.

Demographic Allee effects may exist if population dynamics (i.e. per capita population growth rate), are positively affected by population or group density. To test for a demographic Allee effect, we examined the relationship between per capita population growth rate, calculated as the change in population density from year t to year $t + 1$, and group and population density.

Testing for intergroup interactions

In order to test whether inter-group interactions such as immigration and emigration rates are related to group size, we conducted analyses of per annum immigration and emigration events. For every year, we calculated the number of adult individuals who immigrated or emigrated from each group. All changes in group size (e.g. death) that weren't due to

immigration or emigration were excluded, and all emigration or immigration events that were for a period of less than 30 days (i.e. the individual left the group it joined or returned to the group it left) were also excluded. A group that experienced no immigration or emigration events during the focal year was scored as zero. We used group size and population and group density as predictor terms that may affect immigration and emigration rates.

Data analysis

Statistical analyses were conducted using IBM SPSS statistics version 22.

To test for component Allee effects (annual reproductive rate), and factors influencing immigration and emigration rates, we used Generalised Mixed Models with a poisson distribution. To test for group Allee effects (probability of group persistence per annum), we conducted model selection using Generalised Mixed Models with a binomial distribution; group identity and breeding year were included as random terms. In all of these analyses we compared candidate models (group size and population and group density) using Corrected Quasi Likelihood under independence criterion (QICc, Pan 2001). All candidate models (group size and group and population density) were compared to the QICc of the basic model (with no predictors). The best models were checked for significance using 95% confidence intervals (CI). A term was not considered a good predictor of data patterns if its CIs did intersect zero (Burnham and Anderson 2002).

To test for per capita population growth rate (a demographic Allee effect) we used Generalised Linear Models with a normal distribution. We compared candidate models (group and population density) using Akaike's Information Criterion corrected for small sample size (AICc. (Burnham and Anderson 2002) We used the same criterion for selection of variables as described above for the QICc.

To test for Population and group demographic trends over time we used linear regressions (*sensu* Martin and Maron 2012)

Results

Population and group demographic trends over time

Group size ranged from 3-17 individuals with an average ($\pm$ SE) of 5.54 ± 0.30 adult individuals per group. Yearly group density per km^2 ranged from a minimum of 0.31 groups/ km^2 in 2012 to a maximum 0.73 groups/ km^2 in 1988, with an average of 0.54 ± 0.02 groups/ km^2 . Yearly population size ranged from a minimum of 1.25 individuals/ km^2 in 2012 to a maximum of 5.62 individuals/ km^2 in 1986, with an average 3.09 ± 0.21 individuals/ km^2 . The number of groups per km^2 significantly declined over time ($F=59.96$ $R^2=0.64$, $p<0.0001$, Fig. 1a), as did average group size ($F=15.49$, $R^2=0.32$, $p<0.0001$ Fig. 1b). Per capita population growth rate showed a nearly significant decrease over time ($F=3.72$, $R^2=0.11$, $p=0.06$ Fig. 1c). However, there was no significant decline in the annual reproductive rate of breeding individuals, ($F=1.68$ $R^2=0.05$, $p=0.20$, Fig. 1d)

The presence of a component Allee effect

In total, we collected complete and accurate data on 358 breeding years from 43 different groups. The likelihood of fledging higher numbers of offspring in a given year increased with group size (Table 1, Fig. 2). We found no effect of population or group density on annual reproductive rate (Table 1).

Group Allee effect

We calculated the probability of group persistence for 660 group years for 43 groups. The likelihood of a group to survive a given year increased with group size (Table 2, Fig. 3). We found no effect of population or group density on group persistence probability (Table 2).

Demographic Allee effect

We calculated per capita population growth rate for all groups in the study region, resulting in 908 group years from 79 different groups. Per capita population growth rate increased with population density (Table 3, Fig. 4).

Intergroup interactions

We analysed immigration and emigration rates for 618 group years from 43 groups over the time period spanning 1978-2013. Immigration ranged from 0-6 adult individuals per group, with an average of 0.45 ± 0.03 joining a group per year. Emigration ranged from 0-7 with an average of 0.88 ± 0.05 individuals emigrating from a group per year. Group size was the best predictor for both immigration and emigration events, where immigration events happened primarily in small groups, while emigration was primarily observed in large groups (Table 4. Fig 5).

Discussion

Although the presence of both component and group-level Allee effects have recently been described for several cooperatively breeding species (e.g. Somers et al. 2008; Bateman et al. 2011; Bateman et al. 2012; Angulo et al. 2013), empirical evidence for demographic Allee effects have not yet been described for any cooperative breeder. Our finding that per capita population growth rate is positively related to population density reveals that a demographic Allee effect exists in our population. A demographic Allee effect in cooperative breeders may occur when individual survival and reproductive success are dependent on group size (i.e. component and group Allee effects), therefore, our finding of an overall decrease in average group size in our population may suggest that a component and/or a group-level Allee effect have reduced reproductive success and group persistence, which eventually led to a

demographic Allee effect. Our findings support the model suggested by Courchamp et al. (2000), that cooperators in nature are subject to population-level Allee effects. According to this model, component and group-level Allee effects should “scale up” to the population level. Surprisingly, this is the first study to support this prediction.

What are the suggested mechanisms that prevent component and group-level Allee effects from becoming a demographic Allee effects (in contrast to the model suggested by Courchamp, Clutton Brock, & Grenfell, 2000)? And why do these mechanisms not exist in the population of Arabian babblers at the Shezaf nature reserve? Stacey & Taper (1992) showed that small populations of Acorn woodpecker (*Melanerpes formicivorus*), are persisting due to small immigration rates from other, independently varying, populations, and Bateman et al. (2012) suggested that any Allee effect present in small groups may be masked by negative density dependence effects present in large groups (i.e. emigration from larger groups to smaller groups due to critical group size effects), and that this will prevent small groups from declining further or becoming extinct. Our data indeed shows that intergroup interactions are related to group size, and immigration from nearby populations does occur at our study site (Keynan 2015). Nevertheless, these dynamics do not prevent the occurrence of a demographic Allee effect in our population. We suggest that these dynamics are not enough to prevent a demographic Allee effect for two main reasons: First, immigration and emigration continue to occur even when groups are small. We showed in a previous study (Keynan 2015) that in certain cases, the relative size of the group is more important than its absolute size. It seems that even though group size is decreasing in our population, what may be a small group in some years becomes a big group in other years, and as long as there are size differences between neighboring groups immigration and emigration will continue. Second, it could be that although immigration from nearby populations exists, mortality rates

287 have become higher during the last few years, or that the habitat in the study site became sub-
288 optimal in a way that groups are less likely to persist.

289 Courchamp et al. (2000) defined three processes that may drive a population of cooperative
290 breeders toward extinction 1. Smaller groups are less likely to persist. 2. Smaller groups
291 produce smaller dispersing cohorts, which may have lower survival rate, or lower dispersal
292 success. 3. When more habitat patches are simultaneously empty, less colonization from
293 other groups is likely to occur because fewer groups produce fewer dispersers. Another
294 process that Courchamp et al. (2000) suggests, and supported by other empirical and
295 theoretical studies (Creel and Creel 1998; Woodroffe and Ginsberg 1998) is that human
296 interference, mainly degradation of the habitat and persecution by humans, reduces the
297 number of potential patches for colonization and the maximum group size for each patch,
298 which eventually leads to a demographic Allee effect. Our data shows that indeed smaller
299 groups are less likely to persist, and a previous study on Arabian babblers have shown that
300 smaller dispersal cohorts are less likely to be successful (Ridley 2012), but further research is
301 needed in order to conclude whether a decrease in the numbers of dispersers exists in our
302 population, in respect to the effect of habitat degradation and human disturbance on our study
303 population, during the past three decades, the entire central Arava region had become heavily
304 cultivated, mainly by horticulture (Hochman et al. 1985), which has reduced the number of
305 habitat patches available for Arabian babblers and may have an effect on group persistence.
306 Further research is needed in order to investigate whether this disturbance serves to increase
307 mortality of young and adults, and lead to a decrease in group size and therefore a component
308 Allee effect that scaled up to a demographic Allee effect.

309 To conclude, in our analysis of a comprehensive, long-term database, we have been able to
310 determine the presence of component, group and demographic Allee effects in a
311 cooperatively breeding species. These findings are of high significance for several reasons.

First, the presence of a component and group-level Allee effect reveals that individual reproductive success and the probability of group persistence are highly dependent on group size, but not on population or group density. This finding is in agreement with previous research (Woodroffe and Ginsberg 1998; Bateman et al. 2012; Angulo et al. 2013), which suggests that group Allee effects are likely to be present in cooperative breeding societies and are thus an additional level of complexity that we need to take into account when studying population dynamics in cooperative breeders. Second, in contrast to previous suggestions (Bateman et al. 2012; Angulo et al. 2013) we found that although the frequency of intergroup interactions are dependent on group size, it is not a sufficient mechanism to buffer between individual fitness components and population dynamics. Finally, our study is the first to find a demographic Allee effect in a cooperative breeding species, suggesting that group performance and per capita population growth rate should be accounted for when studying population dynamics in cooperative breeders.

Ethics

All applicable institutional and/or national guidelines for the care and use of animals were followed. All birds were captured and ringed under a ringing license from the Israeli Nature and Parks Authority, the research was approved by the Israeli Nature and Parks Authority (License numbers 2011/38268, 2012/38711) and by the Australian Research Authority (ARA, License number 2011/038).

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Table 1: Model selection (QICc) of the terms influencing annual reproductive rate. The best fitting model is highlighted in bold

Term	QICC	Δ QICc	B (effect size)	SE	Confidence interval
Basic	611.35	15.87	1.76	0.09	1.59, 1.93
Group size	595.48	0	0.14	0.04	0.07,0.22
Population density (individuals/km ²)	613.28	17.8	-0.02	0.07	-0.16, 0.13
Group density (groups/km ²)	613.01	17.53	0.27	0.59	-0.89, 1.44

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Table 2: Model selection (QICc) of the terms influencing the likelihood of group persistence on an annual basis. The best fitting model is highlighted in bold

Term	QICc	Δ QICc	B (effect size)	SE	Confidence interval
Basic	258.20	38.38	2.97	1.80	2.62, 3.33
Group size	219.82	0	0.89	0.23	0.44, 1.35
Population density (individuals/km ²)	250.23	30.41	0.55	0.18	0.18, 0.92
Group density (groups/km ²)	251.05	31.23	3.49	1.04	1.44, 5.54

Table 3: Model selection (AICc) of the terms influencing per capita population growth rate. The best fitting model is highlighted in bold

Term	AICc	Δ AICc	B (effect size)	SE	Confidence interval	Weight
Basic	-12.95	3.98	1.01	0.03	0.95, 1.08	0.12
Population density (individuals/km²)	-16.93	0	0.06	0.02	0.02, 0.10	0.78
Group density (groups/km ²)	-12.60	4.33	0.32	0.20	-0.01, 0.72	0.10

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Table 4: Model selection (QICc) of the terms influencing annual immigration and emigration rates per group. The best fitting model is highlighted in bold

	Term	QICc	Δ QICc	B (effect size)	SE	Confidence interval
Immigration	Basic	883.26	90.82	-0.801	0.09	-0.98, -0.62
	Group size	792.44	0	-0.26	0.05	-0.36, -0.17
	Population density (individuals/km ²)	885.19	92.75	0.01	0.08	-0.17, 0.03
	Group density (groups/km ²)	885.02	92.58	-0.21	0.65	-1.49, 1.07
Emigration	Basic	1192.95	225.09	-0.13	0.06	-0.26, -6.5E-005
	Group size	967.86	0	0.20	0.01	0.17, 0.23
	Population density (individuals/km ²)	1194.23	226.37	0.03	0.07	-0.09, 0.16
	Group density (groups/km ²)	1194.50	226.64	-0.21	0.50	-1.19, 0.77

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475 **Fig. legends:**

476 • **Fig. 1:** changes in (a) the group density (no. of groups per km²) (b) yearly average of
477 adult group size, (c) per capita population growth rate and (e) yearly average of
478 annual reproductive rate for breeding individuals. Data available for the years 1978-
479 2013. Linear fits are shown when statistically significant

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481 • **Fig. 2:** The relationship between the number of nestlings that fledged per year (as a
482 measure of annual reproductive rate for breeding pair) and group size. Grey area
483 represents 95% confidence intervals

484 • **Fig. 3:** The relationship between group persistence during a given year (0=extinct,
485 1=survived) and group size. Thickness of dots represents the number of observations.
486 Grey area represents 95% confidence intervals

487 • **Fig. 4:** The relationship between per capita population growth rate (number of
488 individuals in the population in year t+1/ number of individuals in year t) and the
489 number of individuals per km² in year t. Grey area represents 95% confidence
490 intervals

491 • **Fig. 5:** The relationship between the number of adults emigrating (full line, black
492 dots) and immigrating (dashed line, white dots) per annum and group size. Grey area
493 represents 95% confidence intervals

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Fig. 1

Fig 2:

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523 **Fig. 3:**

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Fig. 4:

Fig. 5: