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All alloparents are not equally valuable: Primary breeders and group size explain group reproductive success in cooperatively breeding primates.

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Abstract

The effect of a cooperatively breeding group's composition on its reproductive output (GRO) has been difficult to assess across populations and species. Prior research has correlated GRO with age and sex classes, not accounting for uneven sample sizes and pseudoreplication at the group or species level. This study utilizes a multistep modelling approach to assess whether breeding status explains GRO better than age-sex classes among free-ranging saddleback (*Saguinus weddelli*) and emperor tamarins (*S. imperator*) in Peru. Dimension reduction analyses were performed on 6 years of morphometric data to assign breeding status to individuals. Three analytical approaches (GLMM, binomial logistic regression and multinomial logistic regression) were used to model the effects of breeding status on GRO in the current dataset and a historical dataset derived from previous studies of wild callitrichids. Though alloparents have long been considered critical to reproductive success in cooperative breeders, these results indicate that group size and the proportion of primary breeders are the most significant factors contributing to GRO. This indicates that reproductive suppression of subordinate females may even be detrimental to GRO and though additional primary breeding males increased GRO, the addition of secondary breeders, male or female, did not.

Keywords

Callitrichid, cooperative breeding, group composition, reproductive output, breeding status

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1. Introduction

In a cooperatively breeding system offspring receive care from non-biological alloparents [1]. Alloparenting can occur in pair-bonded breeders (e.g. mongoose [2], ~ 9 % of birds [3]), or in groups with multiple adult breeders and reproductive skew (e.g. prairie voles [4], meerkats [5], and humans [6]). In primates, including humans, the frequency of alloparental care predicts social tolerance, which enhances group cohesion [7]. While some studies emphasize the influence of alloparenting [8-10] over prior parental experience [11] on group reproductive output (GRO), others suggest that helpers could be detrimental [12].

Callitrichids are cooperatively breeding nonhuman primates typified by elevated levels of prosociality and social tolerance [13,14]. However, groups vary in how and why they breed cooperatively: previous reproductive output can modulate present litter size [15] and maternal care can vary with helper availability and maternal health [16,17]. While subdominant females could alloparent to gain experience for future offspring, males could alloparent to ensure the success of young they may have fathered [13,18].

Previous studies have assessed the effect of group composition on GRO [13,14,19]. Garber [14] found that average GRO increased with the number of helpers (typically adult males) in *Saguinus mystax*. Among *Leontopithecus rosalia*, average GRO was significantly correlated with average helper numbers in established groups [19]. Koenig [20] confirmed these results across multiple studies on the marmoset *Callithrix jacchus*.

However, past analytical approaches have some disadvantages. First, correlations of average GRO with composition of age-sex classes do not account for uneven sample sizes common to even the best longitudinal datasets on wild callitrichids. We assessed a thirteen-year study on *Saguinus weddelli* [21] with groups of 1-4 adult males and found that 68 % (32/47) of groups had 2 adult males, while only 5 % (2/47) had 3 males, and 2 % (1/47) had four males – disparate sample sizes that preclude using averages to test the effect of age-sex class on GRO (Fig. S1 in Supplementary Materials). Second, statistical models using absolute numbers of individuals in age-sex classes can be confounded by larger groups producing more offspring overall [14,20]. Finally, comparative datasets across several species and with repeated measures from the same social groups need statistical models that can control for species and group level effects.

We surmise that individual breeding status may be a better predictor of GRO than age-sex classes. Despite callitrichids having scent-glands and genitalia that vary according to reproductive status [22,23] and season [24,25], currently there is no reliable procedure for determining breeding status. This is relevant given that subordinate females experience family-induced reproductive suppression, further disconnecting age from reproductive capability [18,26-29]. The diminutive size and relative morphological homogeneity of callitrichids also preclude breeding status determination without the aid of a capture program.

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We used morphological and group composition data from a 6 year mark-recapture study on two callitrichid species to model individual breeding status and assess whether breeding or age-sex classes better explain GRO. Additionally, we compiled historical data on callitrichids to re-analyse GRO in relation to age-sex classes while accounting for the confounding effects of unequal sampling and pseudoreplication.

2. Methods

(a) Study Site and Subjects

We studied 21 groups of free-ranging saddleback tamarins (*Saguinus weddelli*, formerly *S. fuscicollis weddelli* [30]) and emperor tamarins (*S. imperator*) at the Estación Biológica Río Los Amigos (EBLA) in the Madre de Dios Department of southeast Perú across 6 seasons (2010-2015) via mark-recapture (detailed protocol in [31]). At capture, infants were 4 to 7 months old, readily identifiable by facial pelage and dentition. The Peruvian Ministry of the Environment (SERFOR) granted annual research and collection permits, and the Animal Studies Committees of Washington University in St. Louis and the University of Missouri - St. Louis approved protocols. This study follows the Animal Behaviour Society Guidelines [32] and American Society of Mammalogists Guidelines on wild mammals in research [33].

(b) Assigning breeding status:

To determine breeding status, we recorded length and width of genitalia and suprapubic glands and formulated indices of breeding status as follows: vulvar index (VI=length + width), suprapubic gland area (SPA=length * width), average nipple length, and testicular volume (TV=semi-spherical estimate) [24,34]. In 2.4% (8/331) of captures a measurement was not recorded. We avoided omitting these records by inserting the average by breeding status (animals of known breeding status, n=4) or age-sex class (unknown breeding status, n=4).

We mean-centred and scaled all measurements and indices by standard deviation for use in a principal components analysis by species-sex groups (PCA: FactoMiner package in R [35]). Callitrichids typically live in groups with one primary breeding female (PBF), secondary females (SBFs unable to breed in the presence of PBFs), primary or secondary males (P/SBMs), and non-breeders (NBF/Ms). Individual coordinate values from the first two principal components were used in a linear discriminant function analysis (LDA) to model three breeding categories: primary, secondary, and non-breeder. Resampling of individuals occurred 1 to 4 times per animal, with 51.8% captured at least twice. To avoid pseudoreplication, we used mean individual component scores across years for animals with known breeding status (defined as per Table S1) to train the LDA functions. Each species-sex class was checked for normality (q-q normal plots), linear relationships (linear regression), and homoscedasticity between breeding categories (Bartlett's test of homogeneity of variance, $p > 0.05$). Non-breeding males of both species were omitted from the LDA due to limited variance causing heteroscedasticity; but since they were <

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7 months old, this exclusion had no impact on adult and sub-adult male classifications. We calculated the percentage of known individuals that were correctly classified by this PCA-LDA model (Table S2), and used a MANOVA (manova: MASS package in R [36]) to test the null hypothesis that all predicted breeding status groups were indistinguishable based on individual component scores. All statistical analyses were performed in R v.3.2.2 [37].

(c) Group reproductive success

We compiled studies on wild populations of *Saguinus* spp. and *Callithrix jacchus* with published numbers of individuals per age-sex class (NASC) and GRO (historical dataset will be in Section 1 of Dryad). First, we evaluated average GRO per NASC as per [14]. Based on more recent analyses [14,19,20], we also performed Spearman's rank correlations of GRO with NASC and group size. However, correlations are pair-wise, not predictive, and cannot control for group identity or species [38]. Thus, as per [19], we built generalised linear mixed models (GLMMs: lme4 in R [39]) with a Poisson error structure, response variable GRO (ranging from 0-3), and NASCs as fixed factors. We used saturated fixed-effect models to optimise random structures, incorporating group identity, species, and year when they had any effect on the outcome. Minimal models were established using Akaike Information Criterion [40] by backwards non-significant term deletion, retaining terms only if they reduced AIC by two units [41]. Additionally, we constructed mixed-effect logistic regression models with identical terms but a binary response variable (offspring presence/absence), binomial error structure, and a logit link function. Since NASC increases with group size, we also re-ran both sets of models with the proportion of individuals in age-sex classes relative to group size (PASC) as explanatory variables.

Both modelling approaches were repeated on the current dataset using PASC and the proportion of individuals in each breeding class relative to group size (PBC) as explanatory variables. We also performed multinomial logistic regression models with PBC, separating GRO into two levels: 0 to 1 offspring, and 0 to 2+ offspring. Fixed and random factors remained the same for all analyses except multinomial logistic regression, which does not support random factors (multinom: MASS package in R [36]), but our findings indicated that this did not affect the model outcome.

3. Results

(a) Group Demographics

Over 6 years we observed 63 reproductive attempts in 21 groups, including 14 groups of *S. weddelli* sampled for a mean of 2.86 ± 1.35 s.d. years and 7 groups of *S. imperator* sampled for a mean of 3.43 ± 1.27 s.d. years. Mean group sizes (Table 1), adult group sex ratios (males:females) (*S. weddelli*: 1.23 ± 0.63 s.d.; *S. imperator*: 1.65 ± 1.34 s.d.), and GROs (*S. weddelli*: 1.03 ± 0.87 s.d.; *S. imperator*: 0.92 ± 0.88 s.d.) were not significantly different between

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species (Welch's Two Sample t-test, $p > 0.05$). Across the study, 8.7% of all captures were of 1-2 offspring per group, with only one instance of three offspring. We observed 7 instances of multiple primary breeding females present in a single group – four in *S. weddelli* and three in *S. imperator*.

(b) The Breeding Status Model

We modelled the breeding status of 166 animals (106 *S. weddelli* and 60 *S. imperator*) over 323 capture events. Minimum requirements for factor analyses were satisfied, with an average of 19 and 23 samples per variable for the females and males. The two dimensions represented an average of 86 % (range: 82 – 90 %) of total group variation. For all species-sex classes, PCA dimension 1 was determined by all morphological variables and PCA dimension 2 was determined primarily by nipple length in females and suprapubic area and animal weight in males (Tables S3 and S4 in Supplementary Materials).

For animals with known breeding status (57.1 % of *S. weddelli* and 59.5 % of *S. imperator*), the LDA correctly assigned 98.3 % of female *S. weddelli*, 100 % of female *S. imperator*, 76.7% of male *S. weddelli*, and 88.2 % of male *S. imperator* (Fig. 1, Table S2). The LDA classification mismatched one SBF to NBF (*S. weddelli*); four suspected PBMs became SBMs, and three SBMs switched to PBMs (*S. weddelli*); and two PBMs became SBMs (*S. imperator*). The LDA successfully distinguished between breeding classes for females and males of both species (MANOVA, $p < 0.0001$, Table S5). See Table S6 in Supplementary Materials for mean values and ranges of morphological variables per species-sex group.

(c) Group Reproductive Success

Mean GRO in the historical dataset revealed unequal sample sizes per age-sex class with overlapping confidence intervals (eg. mean offspring =1.10 ± 0.87 s.d., CI: 0.94 -1.27 in groups with two adult males while mean offspring = 0.93 ± 0.77 s.d., CI: 0.72 – 1.14 in groups with one adult male) (Fig. 2). Mean group sizes were significantly different in historical datasets for tamarins (4.63 ±1.50 s.d., range: 2 -10, N = 177) and marmosets (8.08 ± 2.96 s.d., range: 3 -15, N = 36) (Wilcoxon Rank-Sum $W = 5325$, $p < 0.0001$), so they were analysed separately. In the historical tamarin dataset, GRO was significantly positively correlated with group size (Spearman's rank correlation ρ (177)=0.260, $p = 0.0006$) and the number of adult females (ρ (177)=0.150, $p = 0.0439$) but not with other age-sex classes. The historical dataset for marmosets yielded no significant correlations across all cases.

In the historical tamarin dataset, group size was a significant factor across all modelling of GRO via GLMM with Poisson errors and logistic regression with binomial errors using NASC and PASC ($p < 0.05$) (Table 2). No other explanatory terms were significant, but the proportion of adult females approached significance using logistic regression of PASC ($p = 0.052$).

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With new data from this study, we could not reject the null model in a GLMM with Poisson errors or binomial logistic regression using PASC (Table 2). We then replaced PASC with PBC, and a model with a Poisson error structure revealed that the proportion of PBFs and group size were significant. A binomial logistic regression indicated that the proportion of PBMs significantly explained the presence of offspring, while both group size and PBFs approached significance. Removal of either PBFs ($\chi^2(1) = 24.4$, $p < 0.0001$) or group size ($\chi^2(1) = 13.5$, $p = 0.0002$) significantly reduced model likelihood. Finally, a multinomial logistic regression on the same dataset revealed that the proportion of PBMs significantly explained the first level (0 to 1 offspring), while group size explained the second level (0 to 2 or more offspring), and the proportion of PBFs approached significance ($p = 0.0522$) (Table 2); again, removal of PBFs significantly reduced model likelihood and increased AIC.

4. Discussion

Like other callitrichids, both study species twinned frequently and formed groups with multiple breeding females [42]. Though these species diverged ~10.07 mya [30], we noted no significant differences between them in mean group size, adult group sex ratios, or mean GRO.

(a) Modelling breeding status

Reproductive status has been evaluated in callitrichids through measurements of their genitalia [25,34,43]. In addition, scent-gland morphology is known to signal oestrus, changes around parturition (*C. jacchus* [44]), and differs by sex [23,45,46]; thus, it is likely correlated with breeding status [23]. However, a method for reliably assigning breeding statuses is missing to date. The proposed model utilised both genitalia and scent gland morphology to assign animals into breeding classes, with a higher success rate in females than males. This sex-difference was likely due to the availability of validated measures in females, such as observed nursing and nipple lengths [34], which were missing for males. Higher resolution on male breeding status would require the inclusion of all or most copulation records, which was not feasible as copulation is cryptic among arboreal primates [47] and of short duration (1-12 s) in tamarins [23]. Nevertheless our model successfully discriminated between breeding categories for all species-sex classes, confirming that all animals of a particular age-sex class did not have equal reproductive capabilities.

(b) Group composition and reproduction

To date, studies on the effect of helpers on GRO among callitrichids have depended on correlations or descriptive statistics, often within small datasets [14,20,48]. Contrary to earlier findings, our analysis of a large historical dataset of tamarin group compositions could not confirm that adult males were positively correlated with GRO [14,20]. However, we detected that the proportion, and not absolute numbers, of adult females approached significance in a logistic regression model. This could be attributed to the singular dependence of reproduction on breeding females and the possible presence of multiple breeding females, which could not be

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confirmed in the historical dataset. Ultimately, group size was the only factor that consistently influenced GRO across all models, and the use of proportions rather than numbers of individuals allowed us to isolate the potential effects of each age-sex class. Larger groups generally resulted in more individuals in each age-sex class, but also allowed for more variation among individuals within classes, which has not been addressed in prior studies.

Among callitrichids and some other primates, there is often a marked disconnect between age and reproductive capability [18,27,29]. When we considered breeding status in the current dataset, we found that the proportion of PBFs and PBMs significantly impacted GRO (Table 2), but that SBFs and SBMs (who could be subadults or adults) did not. Secondary breeders only facilitated GRO indirectly by increasing group size. These insights raise new questions regarding the role of subadults in callitrichids, whose alloparental contributions have been considered integral to GRO [10,19]. In other cooperatively breeding species such as meerkats (*Suricata suricatta*), analyses with multivariate statistical approaches revealed that helpers do not have a direct effect on litter sizes at birth or pup weights at weaning, which were influenced by maternal weight instead [5]. Additionally, among European badgers (*Meles meles*), the impact of helper numbers on GRO was actually mediated by territory quality [12].

These findings shed light on the ultimate processes that lead to the formation of cooperative breeding groups, which demand that certain individuals give up a degree of their own reproductive success in order to maximize that of others. This strategy is highly advantageous to breeding females, who benefit from the protection of large groups while relieving their offspring of competition for resources with other infants**.** Helpers, in return, could benefit if offspring survival increases the number of future helpers (the group augmentation hypothesis [49]).

However, despite the somewhat strict control of reproduction of subdominant females by dominant females in captivity [50], and the reported harassment of breeding subdominant females and infanticide of their offspring in wild groups [51-53], a variety of callitrichid populations contain groups with multiple breeding females [see reviews: 54-56] including this study [23]. Our findings support the idea that maximum GRO is actually hindered by the reproductive suppression of subordinate females, who have little motivation to allomother solely to gain experience for the care of future offspring [15]. Thus, subordinate females may instead avoid dispersing to benefit from the advantages of group living and to increase their likelihood of reproducing by replacing the PBF [62]. That older PBMs have a direct positive effect on reproductive output, while SBMs do not, indicates that offspring may benefit when males are experienced alloparents, particularly for the first litter [11]. To comprehensively assess the roles of both biological and non-biological parents in increasing GRO however, future studies should consider genetic relatedness and alloparenting behaviours of males whose ages have been accurately evaluated.

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Data Accessibility

The datasets supporting this article will be uploaded to Dryad.

Authors' Contributions

GE and MW conceived of and designed the study. MW determined the initial breeding status models, collected field data and drafted the manuscript; GE collected field data, carried out the statistical analyses, and drafted the manuscript; ER collected field data and helped draft the manuscript. All authors gave final approval for publication.

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Table 1: Group compositions based on breeding class status. All figures are provided as mean number of individuals ± standard deviation (range).

Species	N	Group Size	PBF	SBF	PBM	SBM	All Juvs	All Males	All Females
S. weddelli	14	4.95 ± 1.63 (3-8)	0.95 ± 0.50 (0-2)	0.90 ± 0.78 (0-3)	1.40 ± 0.98 (0-3)	0.65 ± 0.74 (0-2)	1.03 ± 0.86 (0-3)	2.05 ± 0.90 (0-5)	1.88 ± 0.69 (1-4)
S. imperator	7	5.21 ± 1.41 (3-8)	1.08 ± 0.41 (0-2)	0.67 ± 0.96 (0-3)	1.71 ± 1.23 (0-4)	0.63 ± 0.77 (0-2)	0.92 ± 0.88 (0-2)	2.33 ± 1.20 (0-6)	1.96 ± 1.00 (1-4)

Note: P/S/NBF/M = Primary/Secondary/Non Breeding Female/Male; N = Number of unique groups

Table 2: The optimal models for the historical dataset and the present study using GLMM, binomial logistic and multinomial logistic regression.

Data	*Model*	*Ind. Variable*	*Optimal models*														
			Fixed Factor 1					Fixed Factor 2					Fixed Factor 3				
			F	B	s.e.	χ^2	*P*	F	B	s.e.	χ^2	*P*	F	B	s.e.	χ^2	*P*
TH	G	N/PASC, GS	GS	0.125	0.048	6.770	**0.009**										
TH	BL	NASC, GS	GS	0.397	0.136	8.578	**0.003**										
TH	BL	PASC, GS	GS	0.464	0.142	10.61	**0.001**	pF	2.577	1.326	3.776	*0.052*					
TS	G	PASC, GS	-	All terms in the model failed to converge, so we accept the null model													
TS	BL	PASC, GS	-	All terms in the model failed to converge, so we accept the null model													
TS	G	PBC, GS	pPF	3.559	0.962	13.687	**0.0002**	GS	0.343	0.128	7.150	**0.008**					
TS	BL	PBC, GS	pPF	34.230	19.255	3.160	*0.0596*	pPM	3.971	2.006	3.918	**0.048**	GS	2.679	1.418	3.571	*0.0588*
TS	ML -1	PBC, GS	pPF	27.54	16.58	25.35	0.0967	pPM	3.471	1.666	5.403	**0.0372**	GS	2.206	1.190	15.124	0.0638
TS	ML -2	PBC, GS	pPF	32.31	16.64	25.35	*0.0522*	pPM	3.022	1.700	5.403	0.0755	GS	2.485	1.197	15.124	**0.0379**

Random factors of group identity and year were used to control for repeated measures in all models but multinomial logistic regression. In all cases, the response variable was group reproductive output. Datasets: TH = Tamarin Historical; TS = This Study.
Models: G = GLMM (GRO as discrete numerical variable); BL = Binomial Logistic Regression (GRO as binary outcome); ML= Multinomial logistic (Level 1: 0-1 offspring, or Level 2: 0-2+ offspring)
Variables: N/PASC=Number/Proportion of individuals per age-sex class, PBC = Proportion of individuals per breeding class, GS = Group size
Statistical Output: F=fixed factor, B= estimated slope, s.e. = standard error, Factors: pF = proportion of adult females, pPF/M = proportion of primary breeding females/males

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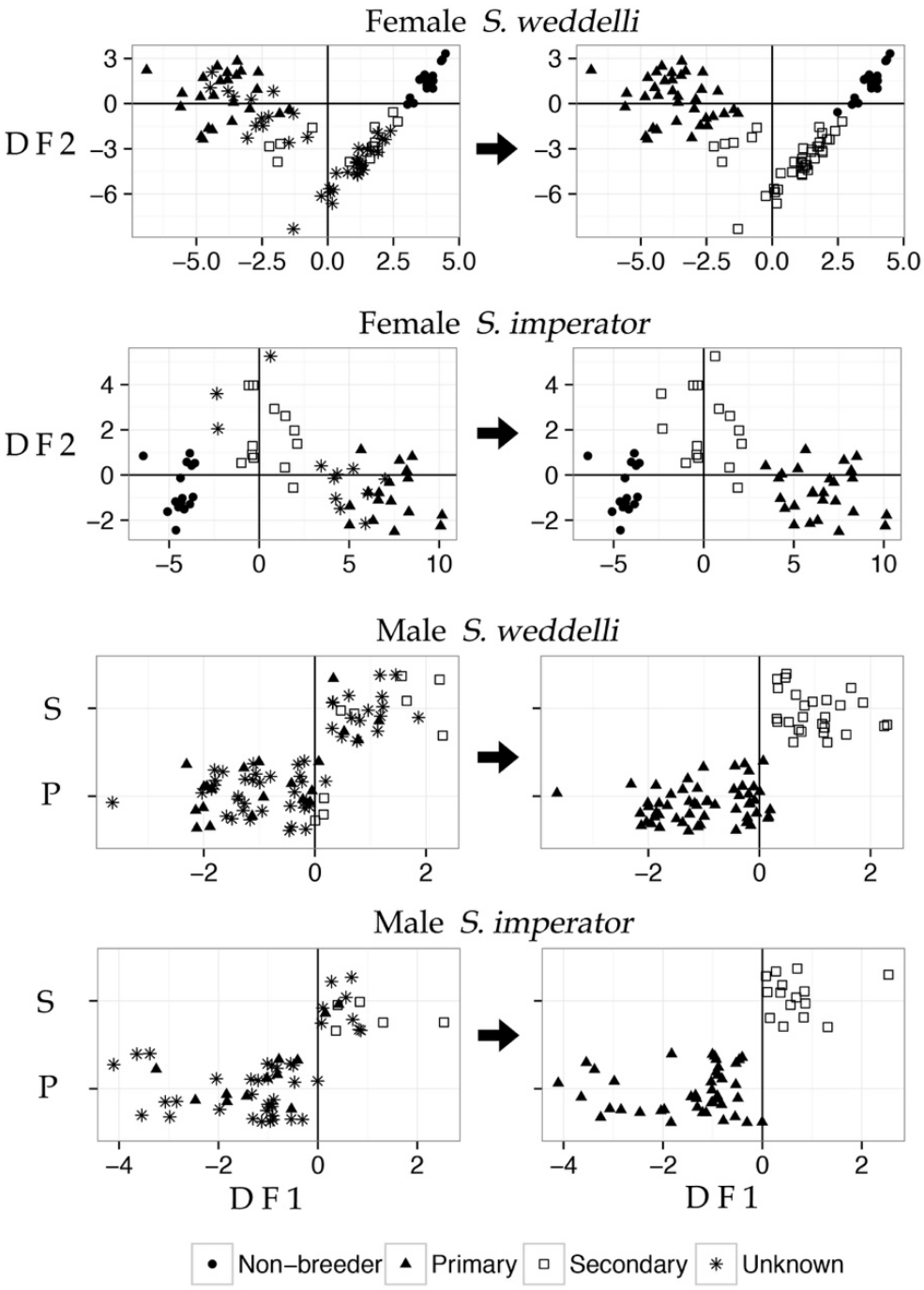

Figure 1. Breeding status by species and sex before (left) and after (right) implementing the PCA-DFA assignment model. Individuals of uncertain status (star symbol) are assigned to a category based on reproductive morphology and weight. Female categories are differentiated by discriminant functions 1 and 2 (DF1 & DF2), while male primary (P) and secondary (S) breeders are differentiated by DF1 only; non-breeding males were removed from the DFA

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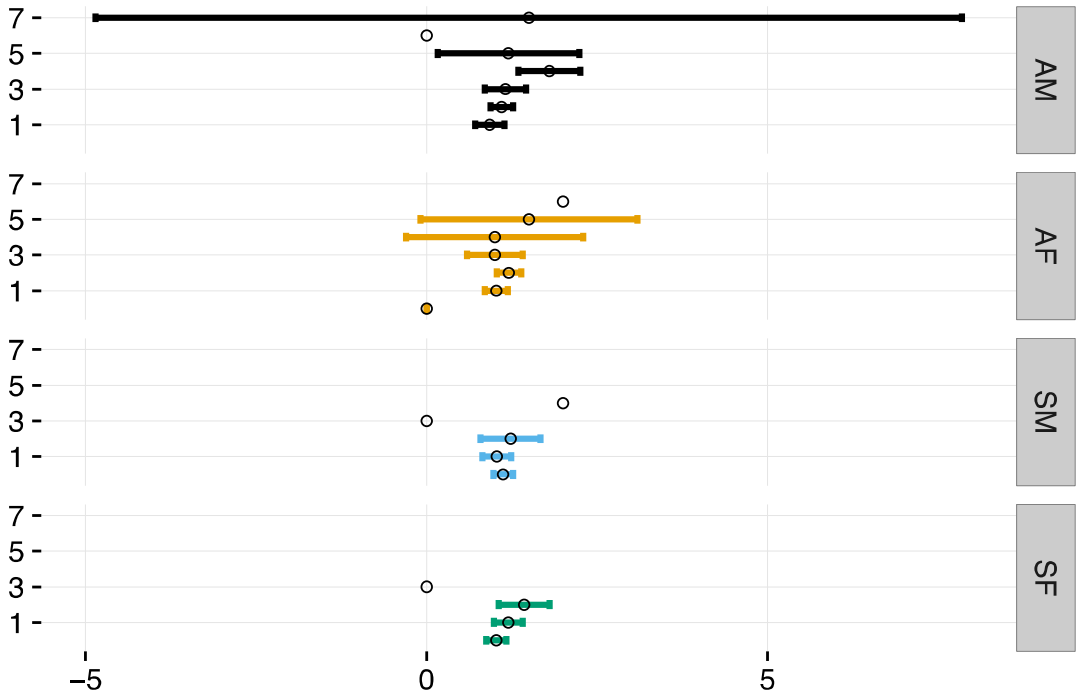

Figure 2. Average number of dependents (circles), with 95% C.I. (lines) depending on the number individuals from each age-sex class in the complete historical data set; adult males (AM), adult females (AF), sub-adult males (SM), sub-adult females (SF).

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