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1 **The evolution of sex roles in birds is related to adult sex ratio**

2

3 András Liker^{1,2*}, Robert P. Freckleton¹ and Tamás Székely^{3,4,5}

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6 ¹ Department of Animal and Plant Sciences, Alfred Denny Building, University of
7 Sheffield, Western Bank, Sheffield S10 2TN, UK

8 ² Department of Limnology, University of Pannonia, PO Box 158, 8201 Veszprém,
9 Hungary

10 ³ Biodiversity Laboratory, Department of Biology and Biochemistry, University of
11 Bath, Bath BA2 7AY, UK

12 ⁴ Department of Animal Behaviour, University of Bielefeld, PO Box 10 01 31
13 33501 Bielefeld, Germany

14 ⁵ Department for Sociobiology/Anthropology, Johann-Friedrich-Blumenbach Institute
15 for Zoology & Anthropology, University of Göttingen, Kellnerweg 6, D - 37077
16 Göttingen, Germany

17

18 * Correspondence should be addressed to A.L. (a.liker@sheffield.ac.uk)

19

20 **Sex-role reversal represents a formidable challenge for evolutionary biologists,**
21 **since it is not clear which ecological, life-history or social factors facilitated**
22 **conventional sex roles (female care and male-male competition for mates) to be**
23 **reversed (male care and female-female competition). Classic theories suggested**
24 **ecological or life-history predictors of role reversal, but most studies failed to**
25 **support these hypotheses. Recent theory however predicts that sex-role reversal**
26 **should be driven by male-biased adult sex ratio (ASR). Using phylogenetic**
27 **comparative analyses, we test this prediction for the first time. Consistent with**
28 **theory, both mating system and parental care are strongly related to ASR in**
29 **shorebirds: conventional sex roles are exhibited by species with female-biased**
30 **ASR, whereas sex-role reversal is associated with male-biased ASR. These results**
31 **suggest that social environment has a strong influence on breeding systems and**
32 **therefore revealing the causes of ASR variation in wild populations is essential**
33 **for understanding sex role evolution.**

34

35

36 One of the fundamental patterns in animal social behaviour is that females tend to be
37 the caring sex, whereas males compete for access to females¹⁻³. Our understanding of
38 what determines these conventional sex roles is challenged by the reversal of sex roles
39 in a number of organisms: the males contribute more to care than females, whereas
40 the females compete for males^{1,2,4}. In sex-role reversed species the females are often
41 larger and more ornamented than males, whereas the males may have specific
42 adaptations for caring for eggs and young^{2,4,5}. Sex-role reversal is taxonomically
43 widespread occurring in insects, fishes, amphibia and birds^{1,4}.

44

45 Sex-role reversal has been a formidable puzzle for evolutionary biologists ever since
46 Darwin⁶, because it is not clear why males under some circumstances provide most
47 (or all) parental care, and why competition for mates should be stronger among
48 females than among males^{1,2,7,8}. Previous hypotheses of sex-role reversal focused on
49 specific ecological and life-history characteristics, such as temporal and spatial
50 variation in food resources, offspring predation and breeding dispersal^{1,9}. Empirical
51 evaluations, however, almost uniformly rejected these hypotheses^{1,9-11}. Indeed, the life
52 histories and ecology of sex-role reversed species are so diverse that it is hard to
53 imagine common environmental circumstances that have led to the evolution and

54 maintenance of sex-role reversal. Species with reversed and conventional sex roles
55 may breed side-by-side sharing much of the environment. Examples include habitats
56 as diverse as the Arctic tundra (phalaropes *Phalaropus* spp. versus calidrine
57 sandpipers *Calidris* spp.¹²) and tropical swamps (African jacana *Actophilornis*
58 *africanus* versus lesser jacana *Microparra capensis*¹³). Higher potential reproductive
59 rates of females have been shown to correlate with more intense mating competition
60 among females in species where only males care for the offspring⁸, although this
61 relationship does not reveal the ecological, life-history or social predictors that have
62 facilitated the evolution of male care in the first place.

63

64 Recent theoretical models put breeding system evolution in a different perspective by
65 showing that adult sex ratio (expressed here as the proportion of adult males in the
66 adult population, ASR) has a major influence on mating competition, mating systems
67 and parental behaviour^{14,15}. These models predict that the rarer sex is under selection
68 to provide less care; for instance, male-biased ASR should facilitate male-biased
69 parental care (henceforth, male care) and thus reversal of conventional parental roles,
70 whereas female-biased ASR is predicted to favour female-biased care (henceforth,
71 female care)^{14,15}.

72

73 Evolutionary changes in mating and parental behaviour are predicted to respond to
74 ASR because if there are substantially more males in the population than females,
75 males have low chances of finding a new mate. Under such circumstances the best
76 strategy for a male may be to provide care for the offspring, rather than desert the
77 female after copulation and face stiff competition in acquiring a new mate. Given that
78 the male cares and the ASR is male-biased, the females can desert the brood and
79 acquire new mates.

80

81 Testing these predictions in wild populations, however, has been challenging. The
82 predictions are difficult to test in a single species, because most species do not exhibit
83 sufficient variation in sex roles and ASR, although one component of sex roles,
84 female social mating system, has been shown to correlate with ASR in dunnoek
85 *Prunella modularis*¹⁶. A multi-species comparative approach is needed, in which the
86 variation in sex roles is compared across a set of species that differs in ASRs.

87 However, such tests have to date been limited by the lack of data on ASR, mating

88 system and parental care from a group of organisms that exhibit both reversed and
89 conventional sex roles.

90

91 Here we provide the first evidence that ASR correlates with parental care and social
92 mating system consistently with the theoretical predictions using shorebirds
93 (Scolopaci and Charadrii, sandpipers, plovers and allies). Shorebirds are eminently
94 suitable for testing theoretical predictions of breeding system evolution, since they
95 exhibit unusual diversity in mating system and parental care, including some of the
96 textbook examples of sex-role reversal^{1,2,11}. We carried out a comprehensive search in
97 primary publications, reference books and online resources for data on ASR, social
98 mating system and parental care, with special attention to species that have been
99 reported to exhibit sex-role reversal. We tested whether ASR predicts mating systems
100 and parental care using Phylogenetic Generalised Least Squares^{17,18}. Although data on
101 ASR from wild populations are difficult to obtain¹⁹, the information now available for
102 shorebirds permits tests of the theoretical predictions using statistically robust sample
103 sizes.

104

105

106 **Results**

107 **Relationships between adult sex ratio and components of sex roles.** ASR is
108 significantly associated with social mating system: sex-role reversed species like most
109 jacanas (Jacanidae) and phalaropes that exhibit female polygamy and female-female
110 competition for mates typically have strongly male-biased ASR, whereas species with
111 male polygamy such as Northern lapwing *Vanellus vanellus* and ruff *Philomachus*
112 *pugnax* have female-biased ASR. The relationships between social mating system and
113 ASR are significant when we use polygamy frequencies (Fig. 1a), and a robust proxy
114 variable for mating system, polygamy scores (Fig. 1b).

115

116 Consistent with theoretical expectations, ASR also correlates with the relative
117 contribution of sexes to parental care, since male care is associated with male-biased
118 ASR (Fig. 1c). In addition, differences in the duration of care provided by males and
119 females, another proxy for parental roles, are also significantly related to ASR (Fig.
120 1d).

121

122 **Sensitivity analyses.** These results are not sensitive to a specific phylogenetic
123 hypothesis, or potentially confounding variables. The aforementioned results are
124 highly consistent between alternative phylogenetic hypotheses and different branch
125 length assumptions: the four key tests remain highly significant by using 100
126 randomly selected trees from the most recent avian phylogeny²⁰ (Supplementary Fig.
127 S1 online), or using alternative phylogenies of shorebirds (Supplementary Table S1
128 online).

129

130 We ascertained whether the genetic mating system of shorebirds may confound the
131 relationships between ASR, social mating system and care. However, by adding extra-
132 pair paternity (EPP) to the predictive models, the direction of relationship with ASR
133 remains consistent in all four cases, remaining statistically significant (or marginally
134 significant) in three out of four phylogenetically corrected correlations (mating system
135 bias: $r = -0.60$, $P = 0.06$; mating score bias: $r = -0.71$, $P = 0.02$; parental care bias: $r =$
136 0.66 , $P = 0.03$; care duration bias: $r = 0.43$, $P = 0.11$, $n = 10$ species in all analyses).
137 Collectively, the latter results strongly support the predicted relationships between
138 ASR, mating system and parental care (Fisher's combined probability test, $\chi^2 = 24.8$,
139 d.f. = 8, $P = 0.002$).

140

141 We also tested whether breeding density, the only ecological correlate of male care
142 demonstrated previously²¹, could influence the mating system, parental care and ASR
143 relationships. However, ASR remains strongly associated with both mating system
144 and parental care when breeding density is added to the models (Supplementary Table
145 S2 online).

146

147 ASR has been estimated using different methods in the field (see Methods), and we
148 tested whether different estimation methodology may have biased the results.
149 Nevertheless, by splitting the analyses into two subsamples (either using direct counts
150 of breeding birds, or using ASRs estimated by all other methods, see Methods) both
151 effect sizes and the direction of relationships remain consistent with those for the
152 whole species set. The relationships remain statistically significant (or marginally
153 significant) in most cases (Supplementary Table S3 online), and collectively provide a

154 strong support for the predictions (Fisher's combined probability test, $\chi^2 = 46.6$, d.f. =
155 16, $P < 0.001$).

156

157 Furthermore, different detectability of the sexes, a potential confound of field
158 estimates of ASR¹⁹, is not likely to bias our results: the more polygamous sex is
159 expected to be more conspicuous due to elaborate plumage, displays and general
160 activity², that would potentially bias ASR estimates towards the direction opposite to
161 our findings (i.e. biasing ASR estimates toward the polygamous sex).

162

163 **Sex-specific results.** The relationships between mating system, parental care and
164 ASR may be due to changes in behaviour of males, females or both sexes. We
165 investigated these propositions by focusing on the behaviour of males and females in
166 separate analyses. Intriguingly, the behaviour of both sexes responds to variation in
167 ASR, since male-biased ASRs are associated with female polygamy and male care,
168 whereas female-biased ASRs are associated with male polygamy and female care
169 (Fig. 2).

170

171

172 **Discussion**

173 Taken together, here we show for the first time that ASR is strongly associated with
174 both social mating system and parental care across bird species, and the explanatory
175 power of the phylogenetically corrected models is relatively high ($R^2 = 0.48 - 0.62$).
176 Our results also reveal that both male and female behaviour show evolutionary
177 responses to ASR, suggesting evolutionary flexibility in both mating and parental
178 behaviour in both sexes. This is also reflected by the fact that flexible sex roles may
179 exist even within a single species (e.g. Kentish plover *Charadrius alexandrinus*²²,
180 Temminck's stint *Calidris temminckii*²³). We propose that the evolutionary flexibility
181 of both sexes to provide full care on their own, and variation in ASR among species
182 are among the key factors that facilitate the evolution of diverse sex roles^{11,24}.

183

184 Although in this paper we focused on sex role reversal, our results also show that
185 ASR is related to sex roles in general: it is associated with mating and parental
186 behaviour through the whole range of avian sex roles, from conventional to role-

187 reversed. We conjecture that ASR may influence other aspects of social behaviour.
188 For example, in populations with biased sex ratios homosexual pairings may be more
189 common, and biased sex ratios may also lead to cooperative breeding where the more
190 common sex in the population postpones dispersal, stay in the family and provide
191 help.

192

193 Further studies are needed to identify why ASR is variable across species. Biased
194 ASRs may arise in several ways: there may be a bias in the primary sex ratio (i.e. sex
195 ratio at conception), or males and females may have differential survival during
196 development and maturation, or as adults. Recent studies suggest that offspring sex
197 ratio at hatching is approximately 1:1 in many birds²⁵, therefore sex biases are likely
198 to emerge after birth.

199

200 It is important to emphasise that mating behaviour, parenting and sex ratios may have
201 more dynamic relationships than currently acknowledged^{15,26,27}. First, ASR can affect
202 sex roles (see above), and conversely, reproductive behaviours can also influence
203 mortalities and thus ASR. Following R. A. Fisher's arguments²⁸ we note that
204 mortalities emerging from sexual competition and parental care may influence the
205 form and intensity of these feedbacks. On the one hand, if mortality from care
206 provisioning is high in a population with male-biased or female-biased care, this
207 would reduce the extent of ASR bias in the population. On the other hand, if sexual
208 selection is costly, then this may generate a positive feedback between ASR and sex
209 roles, so that ASR may shift toward more extreme bias¹⁵. It is conceivable, that
210 populations can be locked in an unusual breeding system, because it is the best
211 response to a biased ASR as generated by the breeding system itself.

212

213 Intense sexual competition and care provisioning have substantial energetic and
214 mortality costs^{29,30}, and thus likely that ASR and sex roles can evolve quickly and
215 concurrently in ecological time scales, rather than in a sequential manner over
216 evolutionary time scales (e.g. changes in ASR precedes changes in sex roles, or *vice*
217 *versa*). We propose that these relationships have a complex dynamics and the
218 dynamics itself may contribute to the immense diversity of sex roles and breeding
219 systems in nature.

220

221 Operational sex ratio (the ratio of sexually active males to receptive females, OSR) is
222 often used in the same context as ASR, although it has been suggested that this is
223 mistaken¹⁵. OSR is only equal to ASR if the sexually active periods of adult males are
224 identical with those of adult females. A population with male-biased ASR can exhibit
225 female-biased OSR, and *vice versa*. Whilst ASR is a demographic property of a
226 population, OSR is also influenced by the mating and parental decisions of animals
227 reflecting their “time in” the breeding pool and “time out”^{8,15}. A significance of our
228 present analyses is therefore to point out that a demographic property, the ratio of
229 adult males and females, is closely correlated with mating and parenting behaviour in
230 wild populations. ASR on its own, however, is unlikely to explain all subtle variation
231 in mating system and parenting of animals, since these may also depend on a suite
232 of other factors.

233

234 We propose two further lines of studies to investigate the influence of ASR on sex
235 roles. First, taxa with variable sex roles (e.g. pipefish *Syngnathidae*, poison dart frogs
236 *Dendrobatidae*, tinamous *Tinamidae*^{4,5,8}) are ideal groups to separate the effects of
237 phylogenetic history, ASR, life-history and ecological traits on sex-role reversal: ASR
238 may predict sex roles in these organisms once ecology and life history differences
239 have been controlled for. Second, experiments are needed to manipulate ASR and
240 investigate the corresponding changes in sex roles. Although ASR has been
241 manipulated in the lab, experiments in natural populations, preferably in species with
242 flexible sex roles, are required.

243

244

245 **Methods**

246 **Adult sex ratio** We systematically searched for shorebirds' adult sex ratio (ASR) data
247 in reference works (e.g. Birds of Western Palearctic, Birds of North America), and by
248 extensively searching the primary literature through the Web of Knowledge (using
249 keywords 'shorebird*', 'wader*', and English and scientific names of specific taxa
250 such as 'sandpiper*', 'Calidris', in combination with 'sex ratio*' and 'ASR'). We
251 calculated ASR as the ratio of adult males to all adults (males plus females) in the
252 populations. When several estimates were available for a species, we used their mean
253 value. In intensively studied breeding populations ASR was often based on censuses
254 of individually marked breeding adults. From the non-breeding period we only

255 included data if the ASR estimates were consistent among studies³¹⁻³³. For 14 species
256 ASR data were taken from the original source whereas for an additional four species
257 ASR was calculated using the data from the original sources. By restricting the
258 analyses to the former 14 species, our results do not change qualitatively
259 (Supplementary Table S4 online). In two species (*Jacana spinosa*, *Metopidius*
260 *indicus*), separate estimates were available for (i) breeding birds, and (ii) breeders plus
261 non-breeders; we repeated the analyses using both sets of data and the results
262 remained highly consistent (Supplementary Table S4 online).

263

264 We aimed at obtaining ASR for as many shorebird species as possible including both
265 sex-role reversed and non-reversed species. In the main analyses (Fig. 1a-d), we used
266 all ASR data (i.e. mean values of all estimates regardless of the methods), whereas in
267 the method-specific analyses (Supplementary Table S3 online) we separated estimates
268 into two groups (breeding censuses *versus* others) to maximise the number of species
269 in the latter analysis. All data and references are provided in Supplementary Tables S5
270 and S6 online.

271

272 **Social and genetic mating system** We used two variables to describe social mating
273 systems. First, we recorded the percentages of socially polygamous individuals
274 separately for males and females³⁰, using reference works and primarily literature
275 (Supplementary Tables S5 and S6 online). Both simultaneous and sequential
276 polygamy were included for both sexes, and if both types of social polygamy occurred
277 within a sex, we used their sum. If several estimates of polygamy were reported for a
278 species, we used their mean. We considered males (or females) monogamous if social
279 polygamy was not reported for the given sex. Lekking birds (two species,
280 *Philomachus pugnax* and *Scolopax minor*) do not exhibit social pair-bonds, thus to
281 express the common assumption that male-male competition is intense in lekking
282 species³⁴, we allocated 100% male polygamy for these species. We calculated mating
283 system bias to represent the species' social mating systems as % male polygamy – %
284 female polygamy. We did not find data on polygamy frequency for two species
285 (*Charadrius nivosus* and *Rostratula benghalensis*), so the maximal sample size for
286 mating system bias tests is 16 species.

287

288 Second, we also used mating system scores as a proxy variable of social mating
289 systems for two reasons: (i) these scores are robust to observer errors in frequency
290 estimates, and (ii) to include the two species in the analyses (see above) which did not
291 have frequency data available. We scored the overall incidence of polygamy for each
292 sex on a 0 to 4 point scale³⁵, with '0' corresponding to no (or very rare) polygamy (<
293 0.1% of individuals), '1' to rare polygamy (0.1–1%), '2' to uncommon polygamy (1–
294 5%), '3' to moderate polygamy (5–20%) and '4' to common polygamy (> 20%). For
295 *Ch. nivosus* and *R. benghalensis* we estimated mating system scores using verbal
296 description of their mating behavior and pair-bonds. Mating score bias was then
297 calculated as the difference between the male and female scores.

298

299 Extra-pair paternity (EPP) data were collected from published sources (see
300 Supplementary Tables S5 and S6 online) and presented as % of broods that include
301 extra-pair offspring.

302

303 **Parental care** We used two variables to estimate the role of the sexes in care
304 provisioning. First, we scored the participation of males on a five point scale (0-4) for
305 five types of parental behavior: nest building, incubation, nest guarding (guarding and
306 defending the nest during incubation), chick brooding, and chick guarding (guarding
307 and defending of the brood after hatching)^{30,35}. We did not include chick feeding since
308 most shorebirds are precocial so that the parents do not feed their young. We also did
309 not include post-fledging care because many shorebirds do not care for the fledged
310 offspring, and also because data are limited on post-fledging care. For all types of
311 care, score '0' indicated no male participation (i.e. all care carried out by females),
312 score '1': 1-33% male care, score '2': 34-66% male care, score '3': 67-99% male care,
313 and score '4': 100% male care (i.e. no female care). These scores were based on
314 quantitative data if such data were available (e.g. % incubation provided by males), or
315 on qualitative descriptions of care in the data source. For example, when a source
316 stated that “most brooding is provided by females”, then brooding was scored as 1 to
317 express the small involvement of male. We calculated parental care bias as the mean
318 score of the five parental activities. For three species (*Actitis macularius*,
319 *Coenocorypha aucklandica*, *Jacana jacana*) and an additional one (*R. benghalensis*),
320 we did not find reliable data on some aspect of care, so for these species the mean
321 score was calculated using 4 (or 2) types of care, respectively. Our scoring expresses

322 male care relative to female care, which is directly relevant for quantifying parental
323 sex roles. For example, a score of 4 refers to complete parental sex-role reversal.

324

325 Second, we estimated the duration of parental care for each sex according to how long
326 the adult cared for the offspring. Following a previous comparative study²⁴, the length
327 of incubation and brood care were divided into three periods (scores 1-3 and 4-6). If a
328 parent did not incubate, it was given a score of 0, and if it stayed until the chicks
329 fledged it scored 7. Sex bias in care duration was calculated as male score minus
330 female score.

331

332 In New Zealand snipe *C. aucklandica* both parents care, although after the hatching of
333 the eggs the males and the females divide the brood and care for half of the brood
334 alone. Since this is not entirely the same as biparental care of the brood exhibited by
335 other shorebirds, we investigated the sensitivity of the results to this data point.

336 Nevertheless, the results qualitatively remain highly consistent when this species is
337 excluded from the analyses (Supplementary Table S4 online).

338

339 **Breeding density** We followed Owens²¹ to obtain comparable breeding density data.
340 We searched for maximum breeding density, and took the number of nests or pairs
341 per hectare. Then, we followed Owens' protocol and used a 1-6 points scale²¹ to
342 convert breeding density into density scores. We used breeding density in the analyses
343 in two ways: (i) density scores were included in multivariate models as a predictor in
344 addition to ASR, (ii) log transformed density was included in multivariate models
345 together with log transformed female body mass and ASR; body mass was included in
346 the models because it strongly correlates with density²¹. We repeated the latter
347 analysis with male mass and reached qualitatively consistent results with those using
348 female mass (results not shown).

349

350 **Phylogenetic comparative analyses** We used Phylogenetic Generalized Least
351 Squares (PGLS) with maximum likelihood to find the best fitting λ ^{17,18}. For most
352 analyses, we used a supertree of shorebirds³⁶, from which we pruned species with
353 missing data, and following a recent molecular phylogenetic study we separated *Ch.*
354 *nivosus* from *Ch. alexandrinus*³⁷ (Supplementary Fig. S2 online). This phylogenetic

355 hypothesis is based on recent advances in molecular phylogenetics and morphology,
356 and has been often used in comparative studies of shorebirds.

357

358 We checked the robustness of the results in two ways. First we re-run the key PGLS
359 models using a sample of 100 trees from the most recent comprehensive avian
360 phylogeny²⁰ to which we added *Ch. nivosus* as described above (Supplementary Fig.
361 S1 online). Second, we repeated the analyses using three alternative phylogenetic
362 hypotheses³⁸⁻⁴⁰ (Supplementary Table S1 online). Since branch lengths were not
363 available for the latter trees (either because no branch length were provided, or
364 because we added some of the species to the phylogenetic tree and hence were unable
365 to use the original branch lengths), we used branch lengths estimated by Nee's
366 method as implemented in Mesquite 2.74^{41,42}. To assess the sensitivity of the analyses
367 to the branch length assumption, we repeated the analyses with unit branch length
368 (Supplementary Table S1 online). All analyses were carried out using the 'caper'
369 package in R⁴³. Correlation effect sizes were calculated from the output of the PGLS
370 models⁴⁴. All statistical tests were two-tailed.

371

372

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482

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484

485 **Figure legends**

486

487 **Fig. 1. Relationships between adult sex ratio and components of sex roles in**

488 **shorebirds.** Adult sex ratio (number of adult males / (number of adult males plus
489 females)) is associated with **(a)** mating system bias (% male polygamy – % female
490 polygamy; phylogenetically corrected $r = -0.79$, $P < 0.001$), **(b)** mating score bias
491 (male polygamy – female polygamy; $r = -0.69$, $P = 0.001$), **(c)** parental care bias
492 (mean of male participation in five parental behaviour: nest building, incubation, nest
493 guarding, chick brooding, and chick guarding; $r = 0.70$, $P = 0.001$), and **(d)** care
494 duration bias (male care duration – female care duration ; $r = 0.69$, $P = 0.001$). Panels
495 show species values whereas the regression lines are fitted by PGLS models (red and
496 blue dots represent species with reversed and conventional sex roles, respectively; $n =$
497 16, 18, 18 and 18 species, respectively).

498

499 **Fig. 2. Sex-specific relationships between adult sex ratio and sex roles.**

500 Phylogenetically corrected correlations between adult sex ratio and polygamy
501 frequency in **(a)** males ($r = -0.62$, $P = 0.008$), and **(b)** females ($r = 0.63$, $P = 0.01$),
502 and mating score in **(c)** males ($r = -0.58$, $P = 0.012$), and **(d)** females ($r = 0.49$, $P =$
503 0.04), and care duration in **(e)** males ($r = 0.61$, $P = 0.007$) and **(f)** females ($r = -0.50$,
504 $P = 0.035$). Panels show species values and regression lines fitted by PGLS models
505 (red and blue dots represent species with reversed and conventional sex roles,
506 respectively; $n = 17, 16, 18, 18, 18$ and 18 species, respectively).



