1   **Contrasting parental roles shape sex differences in poison frog space use but not**

2   **navigational performance**

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35   home range, amphibians, poison frogs

36   **Short title:** Sex differences in poison frog spatial behavior

37

38   **Abstract**

39   Sex differences in vertebrate spatial abilities are typically interpreted under the adaptive

40   specialization hypothesis, which posits that male reproductive success is linked to larger home

41   ranges and better navigational skills. The androgen spillover hypothesis counters that enhanced

42   male spatial performance may be a byproduct of higher androgen levels. Animal groups that

43   include species where females are expected to outperform males based on life-history traits are

44   key for disentangling these hypotheses. We investigated the association between sex differences

45   in reproductive strategies, spatial behavior, and androgen levels in three species of poison frogs.

46   We tracked individuals in natural environments to show that contrasting parental sex roles shape

47   sex differences in space use, where the sex performing parental duties shows wider-ranging

48   movements. We then translocated frogs from their home areas to test their navigational

49   performance and found that the caring sex outperformed the non-caring sex only in one out of

50   three species. In addition, males across species displayed more explorative behavior than females.

51   Furthermore, androgen levels correlated with explorative behavior and homing accuracy. Our

52   findings suggest that poison frog reproductive strategies shape space use patterns but not

53   navigational performance, providing counterevidence to the prevailing view of adaptive sex

54   differences in spatial abilities.

55

56   **Résumé (français)**

57   Chez les vertébrés, les différences de capacités spatiales entre les sexes des sont généralement

58   interprétées selon l'hypothèse de la "spécialisation adaptative", selon laquelle le succès reproductif

59   des mâles serait lié à l'utilisation d'un territoire plus étendu leur procurant de meilleures aptitudes

60   à la navigation. Cependant, une hypothèse du "débordement androgénique" propose que

61   l'amélioration des performances spatiales des mâles puisse être en fait, un sous-produit de niveaux

62   d'androgènes plus élevés. Pour différencier ces hypothèses, il semble donc nécessaire d'utiliser des

63   groupes d'animaux pour lesquels il existe des espèces dont les femelles seraient plus performantes

64   que les mâles en raison de leur écologie. Ainsi nous avons étudié les différences entre les sexes et

65   leur interaction avec les stratégies de reproduction, le comportement spatial et les niveaux

66   d'androgènes, chez trois espèces de grenouilles dendrobatoidés *sensu lato*. Nous avons donc suivi

67   des individus dans leurs environnements naturels, et montré que les rôles parentaux déterminent

68   les différences sexuelles dans l'utilisation de l'espace, le sexe en charge des fonctions parentales se

69   déplaçant sur de plus grandes distances. Nous avons ensuite déplacé les grenouilles de leur site

70   d'origine afin de tester leurs performances navigationnelles et nous avons constaté que le sexe en

71 charge des soins parentaux surpasse le sexe qui ne prodigue pas de soins chez une seule des trois
72 espèces. De plus, chez les trois espèces, les mâles ont montré un comportement exploratoire
73 supérieur à celui des femelles. Enfin, les niveaux d'androgènes sont corrélés au comportement
74 exploratoire et à la précision de la trajectoire. Nos résultats suggèrent donc que les stratégies de
75 reproduction des grenouilles dendrobatoidés influencent l'utilisation de l'espace mais pas les
76 performances de navigation, en contraction avec l'hypothèse dominante sur les différences
77 adaptatives entre les sexes dans les capacités spatiales.

78

79 **Resumen (español)**
80 Las diferencias en las habilidades espaciales de machos y hembras en especies de vertebrados se
81 han interpretado comúnmente bajo la hipótesis de la "especialización adaptativa", la cual sugiere
82 que el éxito reproductivo de los machos está ligado a ámbitos hogareños más extensos y a mejores
83 habilidades de navegación. Por otra parte, la hipótesis de la "sobreproducción de andrógenos"
84 propone que un mejor desempeño espacial en los machos podría ser un subproducto de niveles de
85 andrógenos más altos. Estudios que involucren grupos de animales con especies en las que se
86 espera que las hembras superen el desempeño de los machos con base en ciertos rasgos de la
87 historia de vida son cruciales para poder discernir entre estas dos hipótesis. En este estudio
88 investigamos la asociación entre las diferencias en estrategias reproductivas de machos y hembras,
89 el comportamiento espacial, y los niveles de andrógenos en tres especies de ranas venenosas.
90 Seguimos individuos en su ambiente natural para mostrar que los roles contrastantes de machos y
91 hembras en cuanto al comportamiento de cuidado parental moldean las diferencias en uso del
92 espacio entre los sexos, de forma que el sexo encargado de llevar a cabo el cuidado parental
93 presenta movimiento en un rango mucho más amplio. Luego, translocamos ranas a lugares fuera
94 de su ámbito hogareño para investigar su desempeño de navegación y encontramos que el sexo
95 encargado del cuidado parental superó el desempeño del sexo opuesto únicamente en una de las
96 tres especies estudiadas. Adicionalmente, los machos de las tres especies tuvieron un
97 comportamiento exploratorio más marcado que las hembras. Asimismo, encontramos que los
98 niveles de andrógenos se correlacionan con el comportamiento exploratorio y con la precisión para
99 regresar al hogar. Nuestros hallazgos sugieren que las estrategias reproductivas de las ranas
100 venenosas moldean los patrones de uso del espacio pero no el desempeño de navegación,
101 proporcionando

102

Introduction

Sex differences in spatial abilities are well established in mammals, where males tend to have larger home ranges and enhanced navigational skill compared to females (Clint et al., 2012; Gray & Buffery, 1971; Jonasson, 2005; Jones et al., 2003). In a series of comparative studies, sex differences in space use have been linked to reproductive strategy, where polygamous rodents show sex differences in home range size and spatial abilities, but monogamous species do not (Galea et al., 1994; Gaulin et al., 1990; Gaulin & FitzGerald, 1986; Gaulin & Fitzgerald, 1989; Sawrey et al., 1994). Furthermore, across many human ethnic groups, men tend to score higher on spatial tests related to 3D mental rotations, whereas women tend to score better on object location memory (Eals & Silverman, 1994; Silverman et al., 2007; reviewed in Clint et al., 2012; Jones et al., 2003). The adaptive specialization hypothesis has been widely used to interpret these sex differences by arguing that enhanced spatial abilities in males are an adaptive trait linked to fitness, where males with better navigational skills and larger home ranges may have increased reproductive success (Gaulin & FitzGerald, 1986; Gaulin & Fitzgerald, 1989; Jones et al., 2003). In addition, maternal care in mammals may limit space use and exploration in females (Barnett & McEwan, 1973; Sherry & Hampson, 1997; Trivers, 1972). With few exceptions (Costa et al., 2011; Guigueno et al., 2014; Perry & Garland Jr, 2002; Sherry et al., 1993), empirical support for adaptive sex differences in spatial abilities is based on research in mammals, where males typically have larger home ranges than females (but see Mabry et al., 2013; Mysterud et al., 2001; Ofstad et al., 2016). Taxonomically diverse study systems are needed to test the adaptive specialization hypothesis and its broader implications for the evolution of vertebrate spatial cognition.

Clint et al. (2012) challenged the widely accepted adaptive explanations of sex differences. They countered that sex differences in spatial behavior might be a byproduct of sex differences in androgens rather than an adaptation based on reproductive strategies (i.e., the androgen spill-over hypothesis). Higher androgen levels in mammals enhance spatial performance through effects on neural development and plasticity (Dawson et al., 1975; Galea et al., 1995; Isgor & Sengelaub, 1998; Joseph et al., 1978; Neave et al., 1999; Roof & Havens, 1992; Schulz & Korz, 2010; Sherry & Hampson, 1997; Stewart et al., 1975; van Goozen et al., 1995; Williams et al., 1990). In humans, female performance in spatial ability tasks correlates positively with androgen levels and improves with androgen treatments (Aleman et al., 2004; Burkitt et al., 2007; Driscoll et al., 2005). From an

134   adaptationist perspective, this relationship has been viewed as the proximate mechanism for the

135   selection on males' spatial abilities. However, Clint et al. (2012) argued that better spatial abilities

136   in males might be a byproduct of sex differences in androgens unrelated to selective pressures on

137   spatial behavior and reproductive success. As mammals have limited diversity in reproductive

138   strategies, we lack comparisons with species where females, which have lower androgen levels,

139   have larger home ranges and are expected to have better spatial abilities than males. To disentangle

140   the effect of androgens and life-history traits on sex differences in spatial behavior, we need

141   comparative research in groups of animals where either males or females among closely related

142   species have more complex spatial behavior.

143

144   Fish and amphibians show a remarkable variety of mating strategies and parental sex roles

145   compared to mammals and birds, including widespread polyandry and male uniparental care

146   (Duellman, 1989; Gross & Sargent, 1985; Helfman et al., 2009; Schulte et al., 2020; Wells, 1977;

147   Zamudio et al., 2016). Such behavioral diversity provides natural comparison groups to test

148   alternative hypotheses about sex differences in spatial abilities. In Neotropical poison frogs

149   (Dendrobatoidea), male and female uniparental care, biparental care, and flexible parental sex roles

150   occur among closely related species (Schulte et al., 2020; Summers & Tumulty, 2014; Weygoldt,

151   1987). Poison frog parental care involves complex spatial behavior, where parents navigate the

152   rainforest to transport tadpoles from terrestrial clutches to pools of water (Beck et al., 2017;

153   Pašukonis et al., 2019; E. Ringler et al., 2013). Poison frogs show well-developed spatial cognition

154   and rely on spatial memory to relocate home territories and tadpole deposition sites (Beck et al.,

155   2017; Liu et al., 2016, 2019; Pašukonis et al., 2014, 2016; Stynoski, 2009). Male tadpole transport

156   is the ancestral and most common form of parental care in poison frogs (Carvajal-Castro et al.,

157   2021; Summers & Tumulty, 2014; Weygoldt, 1987), but female transport and flexible parental

158   roles have evolved in some species (E. K. Fischer & O'Connell, 2020; E. Ringler, Pašukonis, et

159   al., 2015). In species where females perform parental care, frogs place their tadpoles in small,

160   resource-poor nurseries. Females frequently return to these pools to supplement the tadpoles' diet

161   by provisioning with unfertilized eggs (Brust, 1990; Summers & Tumulty, 2014). All these

162   parental behaviors require well-developed spatial memory and navigation abilities. Therefore

163   individuals with better spatial memory may have increased reproductive fitness, leading to

164   enhanced spatial abilities in the sex that performs parental care, as proposed by the adaptive

165   specialization hypothesis. Poison frogs also show sex-typical differences in androgen levels, where

166   males have higher androgen levels than females, although androgen levels decrease during tadpole

167   transport in males (E. K. Fischer & O'Connell, 2020). Androgens are also elevated in response to

168   territorial intrusions in males, suggesting that androgens are regulated in these amphibians

169   similarly to other vertebrate taxa (Rodríguez et al., 2022). Thus, comparative studies in poison

170   frogs provide a unique opportunity to understand how parental roles and reproductive strategies

171   shape sex differences in space use and navigational abilities, and how hormones regulate these

172   behaviors.

173

174   Here we report extensive field studies on sex differences in spatial behavior across three poison

175   frog species with contrasting parental sex roles and reproductive strategies: the Brilliant-Thighed

176   Poison Frog *Allobates femoralis*, an inconspicuous frog with flexible but predominantly male

177   parental care, the Dyeing Poison Frog *Dendrobates tinctorius*, an aposematic frog with obligate

178   male care, and the Diablito Poison Frog *Oophaga sylvatica*, an aposematic species with obligate

179   female care. We tracked frogs with miniature tags to quantify sex differences in home range and

180   parental care-associated space in their natural environment. We then quantified the sex differences

181   in navigational performance by experimentally translocating frogs from their home areas and

182   tracking their homing behavior. We also used noninvasive methods to measure androgen levels

183   before and after translocation. Based on the adaptive specialization hypothesis, we predicted that

184   the tadpole transporting sex (males in *D. tinctorius* and *A. femoralis*, females in *O. sylvatica*) would

185   have wider-ranging space use and better navigational performance. Following the androgen

186   spillover hypothesis, we predicted that males would show enhanced navigation regardless of

187   species differences in reproductive strategy.

188

189   **Results**

190   *Sex differences in parental roles predict sex differences in space use*

191   We first quantified the sex differences in space use and the association between movements and

192   parental behavior across three species that differ in parental sex roles (Figure 1). In *A. femoralis*,

193   where males do most parental care duties, the average male home range was 153 % larger and

194   movement extent 172 % larger than females (Table 1 and S1, Fig. 1). The same pattern was

195   reflected in long-term movements based on capture-recapture data (Annex 1). In *O. sylvatica*,

196   where females perform parental care, the average male home range was 56 % smaller and

197   movement extent 57 % times smaller than females (Fig. 1, Table 1 and S1). The same pattern was

198   reflected in movement extent based on short-term tracking at a different study site (Annex 1). In

199   *D. tinctorius*, where males perform parental care, we found no significant sex differences in home

200   range size or movement extent (Fig. 1, Table 1 and S1) based on tracking data, but males showed

201   wider-ranging long-term movements based on capture-recapture data (Annex 1, Fig. S2). Sex

202   influenced the average daily travel of *A. femoralis*, where the best-fit model included sex, behavior,

203   daytime temperature, and random factors, but not in *D. tinctorius* and *O. sylvatica. Allobates*

204   *femoralis* males moved more on days of parental care than on mating days (lsm contrast: $\beta = 1.8$,

205    $P < 0.001$) and other days (lsm contrast: $\beta = 1.9$, $P < 0.001$), but equally between mating days and

206   other days (lsm contrast $P = 0.75$; Fig. 1). *Allobates femoralis* females moved more on days of

207   mating than other days (lsm contrast: $\beta = 0.6$, $P < 0.001$) and were only observed transporting

208   tadpoles once (Fig. 1). *Dendrobates tinctorius* males also moved more on days of parental care

209   than on mating days (lsm contrast: $\beta = 1.3$, $P < 0.001$) and other days (lsm contrast: $\beta = 1.5$, $P <$

210   0.001), but moved equally between mating days and other days (lsm contrast $P = 0.85$, Fig. 1).

211   Daily travel of *D. tinctorius* females did not differ on days of mating from other days (lsm contrast

212    $P = 0.4$, Fig. 1), and females were never observed in the pools or with tadpoles. Daily travel of *O.*

213   *sylvatica* males did not differ between mating days and other days (lsm contrast $P = 0.95$, Fig. 1)

214   and males were never seen transporting tadpoles, but were regularly found near the breeding pools

215   often located inside their territories. Females of *O. sylvatica* moved more on days of parental care

216   than on other days (lsm contrast: $\beta = 0.4$, $P = 0.004$; Fig. 1), but there was no difference between

217   mating days and parental days (lsm contrast $P = 0.8$) or other days (lsm contrast $P = 0.3$). In

218   summary, we found sex differences in space use that reflect sex differences in parental roles across

219   species, and that parental care is associated with the longest movements in all three species.
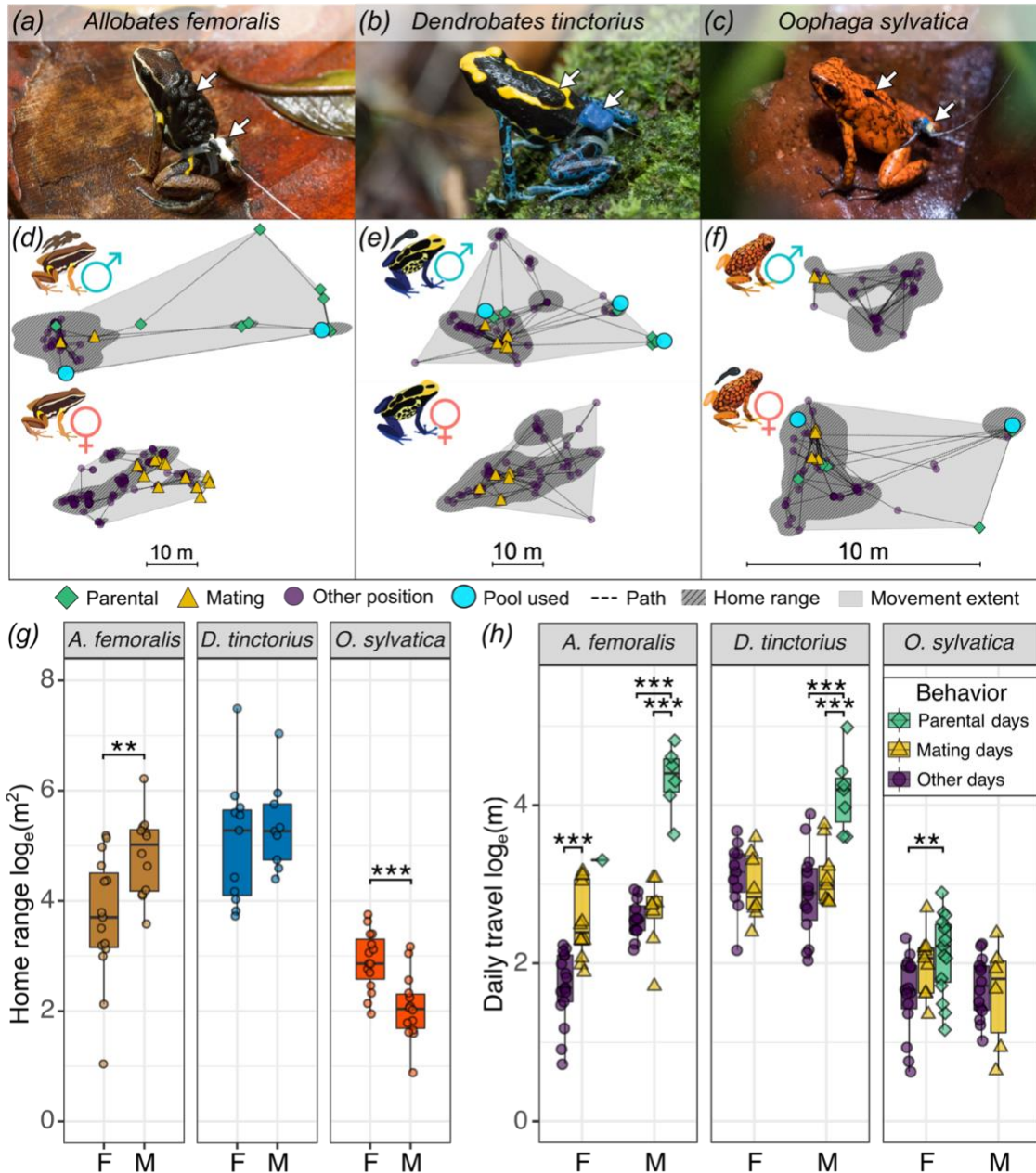
Figure 1. Parental sex roles and behavior drive sex differences in poison frog space use. Male (a, b) and female (c) individuals of each study species transporting tadpoles while wearing a tracking tag. White arrows indicate tadpoles and the tag. (d – e) Examples of representative space use patterns of one individual of each species and sex show different measured space use parameters. We calculated the daily travel as the cumulative distance (line) between all relocations (points) per day; the movement extent (gray shaded area); and the home range representing more intensely used areas (darker hatched area). Frog positions are classified to represent three types of behaviors associated with daily movements: parental behavior (green diamonds), mating behavior (yellow triangles), and other (purple circles). Light blue circles represent pools used for tadpole deposition. Note that the scale is different in the panel for (f) *O. sylvatica*. Boxplots show sex differences in home range size (g), and daily travel (h) between days when parental behavior, mating, or neither were observed. Plot rectangles indicate the lower and upper quartiles with the median line, whiskers extend to 1.5 times the interquartile limited by value range, and dots indicate individuals. As frogs were tracked for multiple days, average values per individual per behavioral category are shown. Days were categorized as pool visits or mating days if the corresponding behavior was observed at least on one relocation of that day. Y-axes are $\log_e$-transformed. Statistical significance levels are indicated as *p $0.05 - 0.01$, **p <0.01, ***p <0.001.

235
236 **Table 1. Home range size model summaries.**

Predictors	*A. femoralis* $\log_e$ (home range)		*D. tinctorius* $\log_e$ (home range)		*O. sylvatica* $\log_e$ (home range)	
	Estimates (CI)	p	Estimates (CI)	p	Estimates (CI)	p
(Intercept)	3.15 (1.1 – 5.2)	**0.004**	5.3 (4.0 – 6.6)	**<0.001**	2.5 (1.6 – 3.4)	**<0.001**
Sex [male]	0.9 (0.2 – 1.7)	**0.015**	0.2 (-0.9 – 1.3)	0.68	-0.8 (-1.3 – -0.4)	**0.001**
Tracking duration	0.06 (-0.1 – 0.2)	0.46	-0.02 (-0.1 – 0.06)	0.62	0.04 (-0.04 – 0.1)	0.36
Observations	25		19		29	
R^2 / R^2 adjusted	0.28 / 0.21		0.02 / 0.0		0.40 / 0.35	

237 Summary of three linear models with $\log_e$-transformed home range size in *A. femoralis*, *D. tinctorius*, and *O. sylvatica*
238 as the response variable, sex as the predictor, and tracking duration (in days) as a covariate. Statistical significance
239 with p < 0.05 is highlighted in bold.
240

241 *Sex differences in parental care do not predict navigational performance*

242 We tested if there were sex differences in navigational performance that reflected sex differences
243 in parental roles and space use across species. When translocated 50 meters, *A. femoralis* males
244 were more likely to return home (81% males, 44 % females), but both sexes of *D. tinctorius* (94%
245 males, 94% females) and *O. sylvatica* (80% males vs 70% females,) were equally likely to return
246 (Fig. 2 and Table 3). When translocated 200 meters, only males of *A. femoralis* (75% males, 0%
247 females) and both females and males *D. tinctorius* (56% males, 39% females), but none of *O.*
248 *sylvatica* were able to return home (Fig. 2 and Table 2). One *O. sylvatica* male could not be located
249 after 6 days and was found back home two days later. *Allobates femoralis* were less likely to home
250 back with higher daytime temperature, but the daytime temperature had no effect on homing
251 success in *D. tinctorius* and *O. sylvatica* (Table 2). Frog weight had no effect on homing success.
252 When translocated 50 meters, *A. femoralis* males explored larger areas than females, but we
253 observed no sex difference in *D. tinctorius* and *O. sylvatica* (Fig. 3, Table S2). When translocated
254 200 meters, males of all three species were more explorative than females (Fig. 3, Table 3). In
255 addition, *A. femoralis* explored less with higher daytime temperature, but the daytime temperature
256 did not affect the explored area in *D. tinctorius* or *O. sylvatica* (Table S2 and 3). Frog weight
257 positively influenced the explored area only in *D. tinctorius* translocated 200 meters (Table 3).
258 Among frogs that returned home, *A. femoralis* males returned more directly and faster from 50
259 meters when compared to females (Fig. 3, Table 4 and S3). In *D. tinctorius*, females returned in

260 more direct paths than males from 200 m (Fig. 3, Table 4). We found no sex difference in *O.*

261 *sylvatica* homing. The same sex-difference pattern in homing accuracy was observed based on

262 angular deviation data (Annex 2). *Allobates femoralis* and *O. sylvatica* returned in less direct paths

263 and slower with higher daytime temperature. *Dendrobates tinctorius* returned slower with higher

264 daytime temperature, but temperature had no effect on trajectory straightness (Table 4 and S3).

265 Frog weight did not affect the homing duration.

266

267 To sum up our navigation experiments, we found that *A. femoralis* males navigate home faster and

268 more accurately, *D. tinctorius* females navigate more accurately from long distances, and males

269 across species display more exploration-related movement compared to females regardless of sex

270 differences in parental care roles.

271
272 **Table 2. Homing success model summaries**

	A. femoralis 50-m homing success		*D. tinctorius* 200-m homing success		*O. sylvatica* 50-m homing success	
Predictors	*Log-Odds*	*p*	*Log-Odds*	*p*	*Log-Odds*	*p*
(Intercept)	107.8 (34.7 – 242.3)	**0.02**	18.7 (-23.9 – 65.4)	0.4	152.65 (-127.6 – 543.3)	0.35
Sex [male]	5.2 (1.7 – 12.4)	**0.03**	1.05 (-1.2 – 3.6)	0.38	1.4 (-1.0 – 4.6)	0.29
Temp.	-4.8 (-10.8 – -1.8)	**0.020**	-0.8 (-2.7 – 0.85)	0.35	-6.5 (-23.3 – 5.5)	0.35
Weight	4.7 (-1.9 – 13.0)	0.19	0.2 (-1.0 – 1.5)	0.74	NA	
Observations	32		32		18	
R^2 Tjur	0.59		0.07		0.10	

273 Summary of three logistic regression models with homing success in *A. femoralis*, *D. tinctorius*, and *O. sylvatica* as
274 the response variable, sex as the predictor, and average daytime temperature (Temp.) and frog weight as covariates.
275 We did not perform statistical comparisons conditions *A. femoralis* 200-m because only males successfully returned;
276 for *O. sylvatica* 200-m because no frogs returned and for *D. tinctorius* 50-m because both sexes return at an equal rate.
277 Weight was excluded for *O. sylvatica* to achieve model convergence. Statistical significance with p < 0.05 is
278 highlighted in bold.

279 **Table 3. Explored area model summaries**

Predictors	*A. femoralis* 200-m $\log_e$ (explored area)		*D. tinctorius* 200-m $\log_e$ (explored area)		*O. sylvatica* 200-m $\log_e$ (explored area)	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
(Intercept)	28.0 (8.7 – 47.4)	**0.006**	5.6 (-7.65 – 18.9)	0.39	30.85 (-97.0 – 158.7)	0.61
Sex [male]	1.5 (0.9 – 2.1)	**<0.001**	1.5 (0.8 – 2.2)	**<0.001**	0.8 (0.02 – 1.7)	**0.045**
Temp.	-1.0 (-1.8 – -0.2)	**0.017**	-0.04 (-0.6 – 0.5)	0.87	-0.9 (-6.4 – 4.5)	0.72
Weight	1.0 (-0.5 – 2.5)	0.19	0.6 (0.2 – 0.9)	**0.004**	-1.4 (-3.2 – 0.3)	0.10
Observations	30		32		15	
R^2 / R^2 adjusted	0.56 / 0.51		0.41 / 0.35		0.38 / 0.21	

280 Summary of three linear models with $\log_e$-transformed explored area in *A. femoralis*, *D. tinctorius*, and *O. sylvatica*
281 as the response variable, sex as the predictor, and average daytime temperature (Temp.) and frog weight as covariates.
282 Statistical significance with $p < 0.05$ is highlighted in bold.
283
284 **Table 4. Homing trajectory straightness model summaries**

Predictors	*A. femoralis* 50-m homing straightness		*D. tinctorius* 50-m homing straightness		*D. tinctorius* 200-m homing straightness		*O. sylvatica* 50-m homing straightness	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
(Intercept)	28.7 (12.6 – 44.9)	**<0.001**	2.0 (-18.9 – 22.9)	0.85	8.9 (-0.7 – 18.5)	0.069	111.0 (25.9 – 196.0)	**0.011**
Sex [male]	0.7 (0.1 – 1.3)	**0.017**	-0.05 (-0.8 – 0.7)	0.89	-0.5 (-0.9 – -0.02)	**0.039**	0.5 (-0.4 – 1.3)	0.30
Temp.	-1.1 (-1.8 – -0.5)	**0.001**	-0.04 (-0.9 – 0.8)	0.93	-0.4 (-0.75 – 0.03)	0.071	-4.8 (-8.4 – -1.1)	**0.011**
Observations	17		22		15		13	
R^2	0.35		0.001		0.39		0.44	

285 Summary of four beta regression models with homing trajectory straightness in *A. femoralis*, *D. tinctorius*, and *O.*
286 *sylvatica* as the response variable, sex as the predictor, and average daytime temperature (Temp.) as a covariates.
287 Statistical significance with $p < 0.05$ is highlighted in bold.
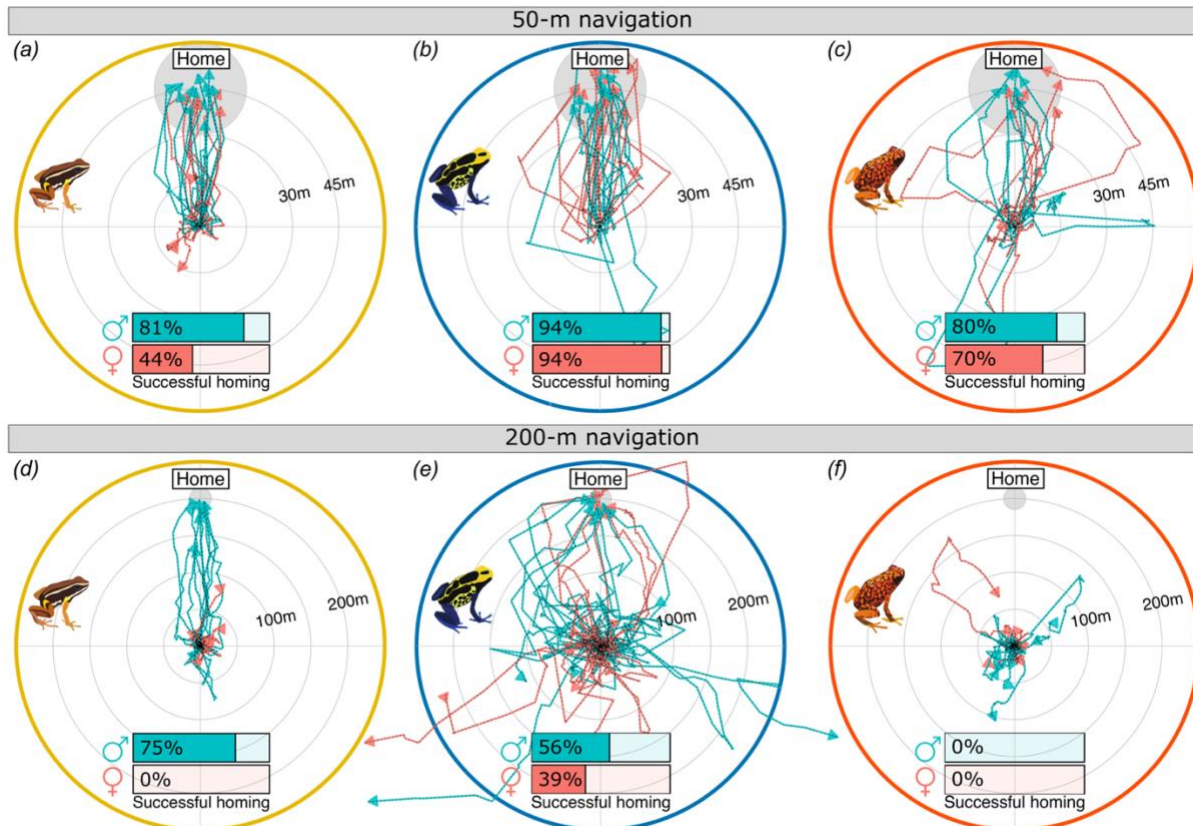
Figure 2. Species and sex differences in movement trajectories of translocated poison frogs. (a - f) Homeward normalized movement trajectories of (a , d) *A. femoralis*, (b, e) *D. tinctorius*, and (c, f) *O. sylvatica* translocated approximately 50 meters (a – c) or 200 meters (d – f) from home. All trajectories are normalized to a common start location (center of the plot) and home direction (top of the plot). The approximate home area is indicated by a gray circle. Each line corresponds to a different individual with male trajectories in teal and female in red. The proportion of each sex that showed homing behavior is indicated on inserted bar plots. Frogs were considered homing if they completed at least 70% of the distance from the release site to the home center within three or six days for 50 m and 200 m, respectively.
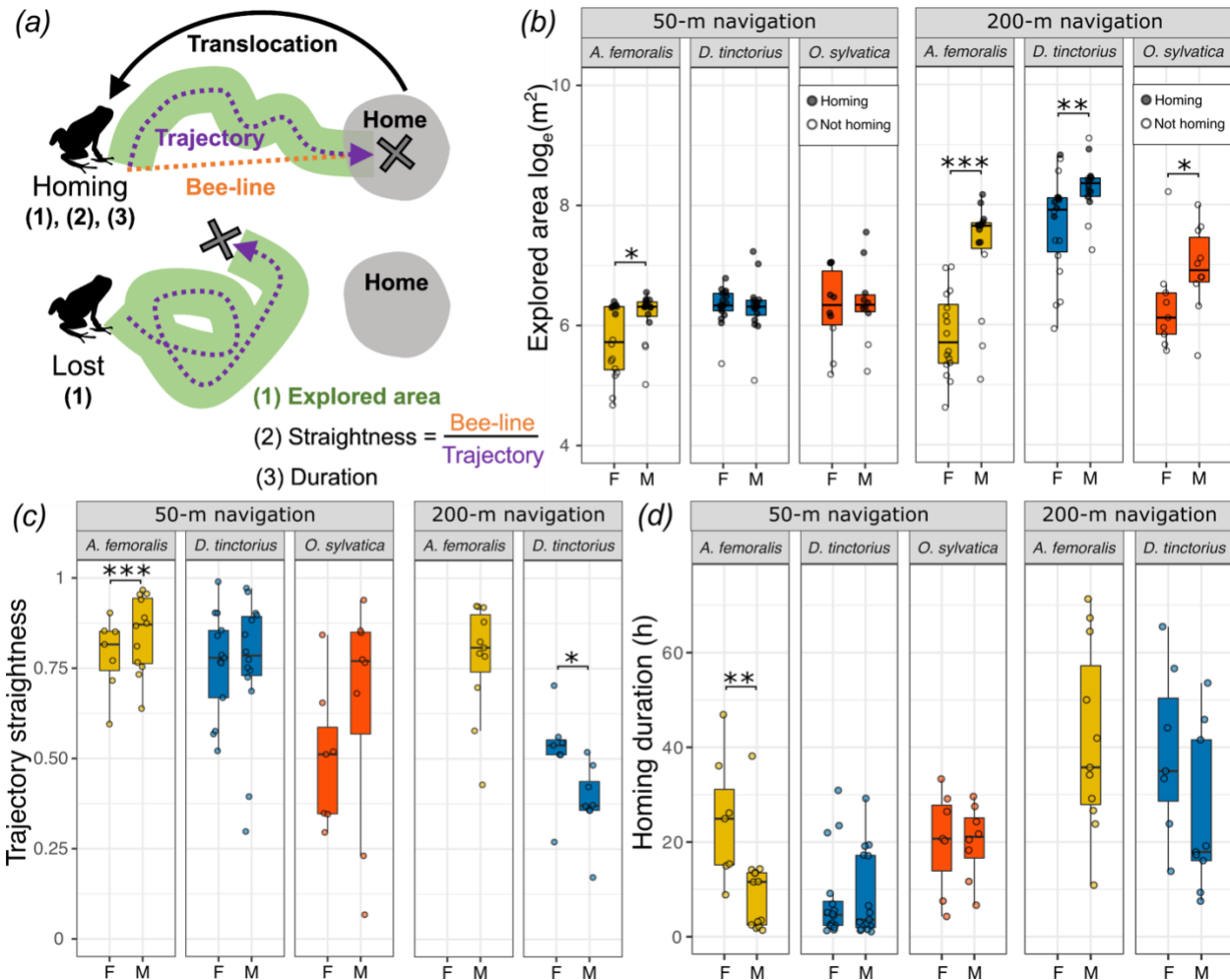
Figure 3. Sex differences in poison frog exploration and navigational performance. (a) Schematic representation of the parameters measured during navigation experiments which are plotted in panels (b - d). Explored area (b), trajectory straightness (c), and homing duration (d) were measured for successful homing, while only explored area (b) were measured for frogs that did not return home. Boxplots show sex differences in (b) explored area ($\log_e$-transformed), (b) homing trajectory straightness, and (c) homing duration. (a) Filled and empty circles indicate individuals that were homing or not. Plot rectangles indicate the lower and upper quartiles with the median line, whiskers extend to 1.5 times the interquartile limited by the value range, and dots indicate individuals. Statistical significance levels are indicated as *p 0.05 – 0.01, **p <0.01, ***p <0.001.
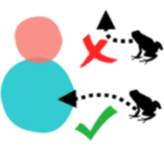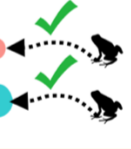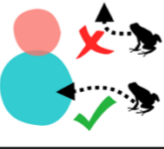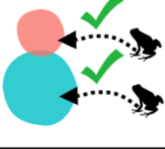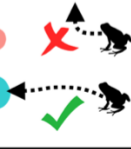
Androgens correlate with navigation-associated behavior

We also investigated the relationship between androgen levels and spatial behavior during the navigation task described above. There was a high inter-individual variation of androgen levels in both sexes of all species, but on average, males showed higher androgen levels in all three species (Fig. 4, Table S4). There were no significant differences between baseline and back-home samples in all three species (Fig. 4, Table S4). Baseline levels did not influence exploration, homing duration, nor trajectory straightness in *A. femoralis* (Fig 4, Table S5). Baseline androgen levels, together with sex, translocation distance, and frog weight significantly predicted exploration in *D.*

315   *tinctorius*, but did not influence homing duration or trajectory straightness (Fig. 4, Table S6).

316   Baseline levels significantly predicted trajectory straightness, but not exploration or homing

317   duration in *O. sylvatica* (Fig. 4, Table S7). The explored area had a significant positive effect and

318   successful homing a significant negative effect on delta androgen levels in *A. femoralis*, but not in

319   *D. tinctorius* and *O. sylvatica* (Table S8).
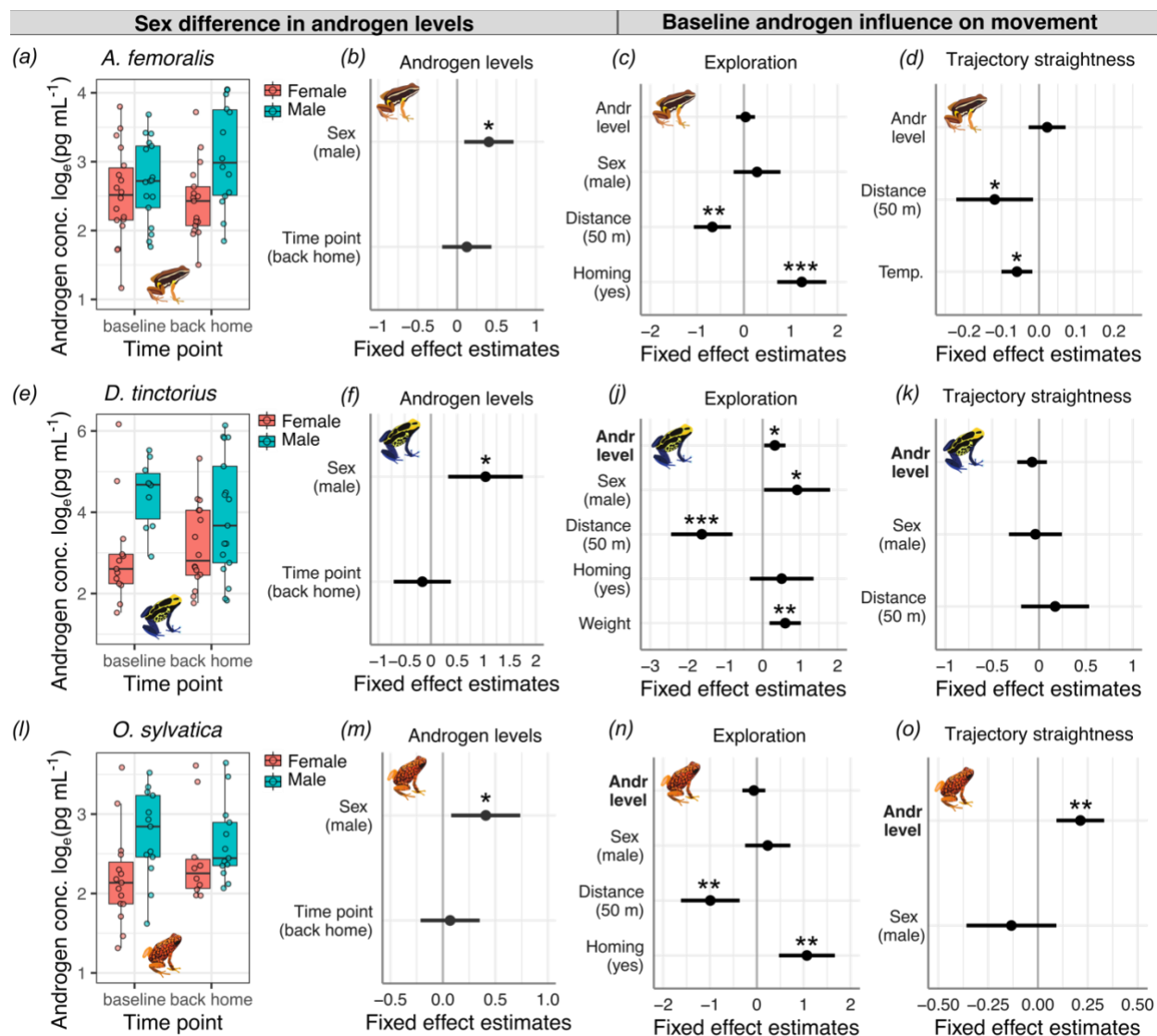
320

321   **Figure 4. Relationships between androgen levels and spatial behavior.** Boxplots show sex differences in water-
322   borne androgen concentration measured before and after the navigational task in (a) *A. femoralis*, (e) *D. tinctorius*,
323   and (l) *O. sylvatica*. The coefficient plots indicate the effect size and confidence intervals of androgen level difference
324   between sexes and the two sampling points for (b) *A. femoralis*, (f) *D. tinctorius*, and (m) *O. sylvatica* and the influence
325   of androgen levels and other factors on exploration (c, j, n) and homing trajectory straightness (d, k, o) in each species.
326   Androgen concentrations are natural $\log_e$-transformed. Statistically significant levels are indicated as *p 0.05 – 0.01,
327   **p <0.01, ***p <0.001.

Figure 5. Summary of sex and species differences in life-history traits, predicted, and observed space use and navigational performance. Red and teal circles represent the space use extent for females and males, respectively, and dotted arrows represent homing after translocations. Orange frame highlights the observed outcomes that differed from the predictions. In all cases, we found no sex differences where differences were expected. *Sex difference only observed in long-term movements and qualitatively in vertical space use (see Annex 1).

Discussion

Sex differences in spatial behaviors are typically interpreted through the lens of the adaptive specialization hypothesis, where larger home ranges and better navigational abilities in males are seen as adaptive traits (Jones et al., 2003). This has been countered with the androgen spillover hypothesis, which suggests that enhanced spatial abilities in males are a byproduct of higher male androgen levels rather than an adaptation (Clint et al., 2012). However, there are no comparative studies where females and males of closely related species have reversed spatial behavior and are expected to show a reversal in spatial abilities. Here, we linked the reproductive strategies, space use, navigational performance, and androgen levels in three species of frogs that differ in which sex performs spatially-relevant parental care tasks that tie spatial accuracy to reproductive fitness (Figure 5). We found that parental care shapes sex differences in space use, but no evidence that sex differences in navigational performance are linked to the reproductive strategy. Importantly, we found that females did not outperform males in *O. sylvatica*, the species with more complex female spatial behavior and larger home ranges associated with female parental care. We also found that males of all three species tended to be more explorative than females, and had higher androgen levels. Moreover, increased androgen levels were associated with higher exploration in

351 two species with male care and navigational accuracy in the species with female care, leaving open

352 the possibility that sex differences in spatial behavior might result from sex differences in androgen

353 levels independent of the differences in parental sex roles.

354

355 *Reproductive strategy shapes species and sex differences in space use*

356 We show that parental care in poison frogs increases the mobility of the caring sex and thus shapes

357 the sex differences in space use. In *D. tinctorius* and *A. femoralis*, males transport tadpoles outside

358 their territory and provide no further care. As we predicted, *A. femoralis* males have a much wider

359 space use than females. Male long-distance movements were primarily observed during tadpole

360 transport and occasional territory shifts, while female space use extent was mainly driven by mate-

361 seeking. This sex difference was less pronounced in *D. tinctorius*, where males did not differ from

362 females in short-term space use based on tracking. Males, however, moved over a wider range

363 based on long-term capture-recapture data (Annex 1). The apparent difference between short-term

364 and long-term data in *D. tinctorius* could be due to real sex differences only emerging in longer-

365 term space use patterns, or the limited statistical power to detect a slight sex difference with a

366 much smaller sample size in the tracking dataset. *Dendrobates tinctorius* males also moved the

367 longest distances on tadpole transport days. During tadpole transport, males also climbed vertically

368 to reach water-filled treeholes high above the ground, which they are known to use for tadpole

369 deposition (Fouilloux et al., 2021). Our space use data does not capture these vertical movements

370 and thus might considerably underestimate *D. tinctorius* male mobility and associated sex

371 differences in vertical space use qualitatively and quantitatively. We could not identify what drove

372 wide-ranging horizontal movements in *D. tinctorius* females, but seeking better foraging sites has

373 been suggested among the movement drivers in *D. tinctorius* (Born et al., 2010).

374

375 Including a species with female uniparental care whose spatial movements are tied to reproductive

376 fitness allowed us to ask whether enhanced mobility could be an adaptive trait linked to parental

377 care. *Oophaga sylvatica* females must remember and revisit tadpole nurseries dispersed over tens

378 of meters to provision their young with trophic, unfertilized eggs (Stynoski, 2009; Summers, 1992;

379 this study). As predicted by the adaptive specialization hypothesis, tracking revealed larger female

380 home ranges in *O. sylvatica*. Females typically moved between several reproductive pools and

381 moved most when visiting or switching between the pool sites. Like *D. tinctorius* males, *O.*

382 *sylvatica* females regularly climbed vertically to water-filled plants up to ten meters above the

383 ground, but these vertical movements are not captured in our space use data. Therefore, our data

384 underestimated the mobility of *O. sylvatica* females and the resulting magnitude of the sex

385 difference. In contrast, males did not climb above two meters, and their movements were restricted

386 to exceedingly small calling territories. It remains unknown if males explore larger areas over the

387 long term, particularly when searching for new territories. Overall, *O. sylvatica* showed more

388 restricted movements than the two species with predominantly male parental care. Several

389 previous studies in poison frogs indicate that species with extended female care, which includes

390 tadpole provisioning, show more restricted space use than closely related species with male

391 uniparental care (Brown et al., 2009; Donnelly, 1989; McVey et al., 1981; Murasaki, 2010;

392 Pašukonis et al., 2019; Summers, 1992). Our data confirm that sex and species differences in space

393 use across poison frogs can be explained, in big part, by species differences in the care-providing

394 sex and the intensity of parental care.

395

396 Research on sex differences in space use has typically focused on differences in mating strategies.

397 For example, male bias in larger home ranges is well documented in rodents, where polygamous

398 species tend to have greater sex differences than monogamous species (reviewed in Clint et al.,

399 2012; Jones et al., 2003). In lizards, a meta-analysis of home range size in 60 species found that

400 males have larger home ranges than females, and suggested that this sex difference is related to

401 the mating system and access to females (Perry & Garland Jr, 2002). Our study shows that parental

402 care can directly influence the space use of the caring sex resulting in sex differences in space use.

403 Parental care has been hypothesized to reduce mobility in the caring sex because the research has

404 focused on maternal care in lactating mammals (Barnett & McEwan, 1973; Sherry & Hampson,

405 1997; Trivers, 1972). In contrast, moving with the offspring or for offspring provisioning is

406 taxonomically widespread in vertebrates and invertebrates (Choe et al., 1997; Clutton-Brock,

407 1991; Kölliker et al., 2012) and can increase mobility in the caring sex, thereby shaping sex

408 differences in space use patterns in taxonomically diverse groups.

409

410 *Species differ in navigational and movement strategy*

411 All three species showed well-developed homing ability, which is consistent with previous studies

412 in amphibians, including various anurans (Arcila-Pérez et al., 2020; Dole, 1968; McVey et al.,

413 1981; Navarro-Salcedo et al., 2021, 2022; Pašukonis et al., 2014, 2018; Pichler et al., 2017;

414 Shaykevich et al., 2021; Sinsch, 1987, 1992) and caudates (Diego-Rasilla et al., 2005; D. Grant et

415 al., 1968; Joly & Miaud, 1989; Phillips et al., 1995; Sinsch, 2007; Twitty et al., 1964; reviewed in

416 Ferguson, 1971; Sinsch, 2006; Wells, 2010). Despite limited movement capacity and sedentary

417 lifestyle, many amphibians appear to share a general ability to navigate home after translocations

418 from distances exceeding their routine movements (Sinsch, 1990, 2014). Moreover, the fact that

419 species showing such tremendous variation in life history share this capacity suggests that well-

420 developed navigational abilities play a fundamental role in amphibian reproduction and survival.

421 Like many other tropical anurans, poison frogs rely on moving between small and scattered water

422 bodies for reproduction, which might have selected for particularly highly developed navigational

423 abilities in this group.

424

425 Our results indicate that navigational and movement strategies differ even between closely related

426 species. The scale and strategy of navigation varied between species and were related to species

427 differences in home range size and reproductive strategy. For example, *O. sylvatica* did not return

428 from longer translocation distances, in line with their much smaller home ranges than in *A.*

429 *femoralis* and *D. tinctorius*. The correlation between home range size and homing performance

430 further supports the hypothesis that poison frogs rely on exploration and spatial learning for

431 navigation (Pašukonis et al., 2014, 2016, 2018). We also found notable species differences in

432 movement and search strategies when animals were navigating home after translocations (Fig. 2,

433 Annex 3, Fig. S4). *Allobates femoralis* tended to stay close to the release site for prolonged periods

434 and then navigate back home via a direct path. Non-homing individuals moved very little and

435 remained close to the release site. However, *D. tinctorius* showed wide-ranging exploratory

436 movements and usually returned home through an indirect and lengthy route. Similarly, even

437 though *O. sylvatica* returned home only from shorter distances, they also showed some wide-

438 ranging exploratory behavior that was never observed in *A. femoralis*. We hypothesize that some

439 of these species differences could be linked to movement strategy differences selected under

440 different predation pressure. *Dendrobates tinctorius* and *O. sylvatica* are brightly colored species

441 that forage actively to acquire their alkaloid-based chemical defenses from the invertebrate diet

442 (Santos et al., 2016; Santos & Cannatella, 2011). Aposematic coloration may reduce predation

443 pressure and the cost of movement while potentially increasing exploration (Carvajal-Castro et al.,

444   2021; Pough & Taigen, 1990; Speed et al., 2010; Summers, 2019; Toft, 1981), allowing different

445   navigational strategies. *Allobates femoralis*, on the other hand, is cryptically colored, non-toxic,

446   and a generalist sit-and-wait forager. Predation pressure is likely to be much higher and the

447   movement more costly for cryptic species, thus potentially selecting more efficient orientation

448   strategies. These differences between closely related species provide a remarkable system for

449   future work on the selective pressures shaping the animal movement and navigational strategy.

450

451   *Navigational performance provides no evidence for adaptive sex differences*

452   The adaptive specialization hypothesis is the leading hypothesis to explain variation in home range

453   size and spatial memory between species and sexes in mammals. It predicts that adaptive sex

454   differences in navigational ability are linked to life history traits. We found no evidence for

455   adaptive sex differences in navigational ability in poison frogs. Contrary to our prediction, we

456   found no sex difference in the navigational performance of *D. tinctorius*, a species with male

457   uniparental care. Not only did males not outperform females, but females even showed slightly

458   more accurate homing trajectories than males when navigating long distances. However, the lack

459   of sex differences in the navigational performance of *D. tinctorius* somewhat fits the limited sex

460   differences in space use observed in this species. Crucially, although females of *O. sylvatica* have

461   larger space use and perform tadpole transport and egg provisioning, we found no sex differences

462   in the navigational performance. Previous research on amphibians has also shown patterns

463   inconsistent with sex differences in spatial abilities being an adaptive trait linked to reproductive

464   strategy. Place discrimination tasks have not revealed consistent sex differences in *Engystomops*

465   *pustulosos*, a frog species where females seek for and move between the males (Liu & Burmeister,

466   2017; Ventura et al., 2019). Using translocation and recapture methods, one recent study in

467   *Andinobates bombetes,* a poison frog with male uniparental care, found no sex differences in

468   homing rates after translocation (Arcila-Pérez et al., 2020). Another recent recapture study in the

469   glass frog *Ikakogi tayrona*, a species with prolonged maternal care and male territoriality, found

470   that only males, but not females, showed homing after translocations (Navarro-Salcedo et al.,

471   2022). Together, our findings and the growing literature on amphibian navigation parallel findings

472   in mammals, where males typically outperform females in spatial tasks or no sex differences are

473   found.

474

475   The only species with marked sex differences in navigational performance was *A. femoralis*, where

476   males were more likely to return home, returned from longer distances, and returned faster and

477   more accurately than females. This finding is partially unexpected because *A. femoralis* females

478   commute between males for reproduction (M.-T. Fischer et al., 2020; E. Ringler et al., 2012) and

479   remember the exact locations of their clutches (E. Ringler et al., 2016). However, because non-

480   homing *A. femoralis* females typically stay stationary, it is difficult to disentangle the lack of

481   motivation from their inability to return home. We expected that *A. femoralis* females would be

482   motivated to return home because they show site fidelity (M.-T. Fischer et al., 2020; M. Ringler

483   et al., 2009; this study) and monitor the presence of their mating partners to eventually take over

484   tadpole transport in case of male absence (E. Ringler, Pašukonis et al., 2015). Indeed, females

485   returned, albeit slower from shorter translocation distances, indicating that they were motivated to

486   return in a sufficiently familiar area. In addition, homing females showed less directed homing,

487   suggesting a sex difference in orientation accuracy. However, males may be more motivated to

488   return home quickly because they risk losing both their territory and all current offspring due to

489   territorial takeovers and potential cannibalism by other males (E. Ringler et al., 2017). We believe

490   that male *A. femoralis* likely have better navigational abilities than females, but the motivational

491   state linked to each individual's current reproductive or parental status may explain some of the

492   sex and inter-individual differences observed in homing performance.

493

494   *Males explore more than females*

495   Males are bolder and more explorative in several species and taxa (e.g., fish: Harris et al., 2010;

496   King et al., 2013; bird: Schuett & Dall, 2009) and multiple adaptive hypotheses have been

497   proposed to explain increased exploration (reviewed in Schuett et al., 2010; Trivers, 1972). Sex

498   differences in exploration tendency could be connected to the sex-biased dispersal observed in

499   different mating strategies, where male-biased dispersal is common in polygamous mammals

500   while female-biased dispersal is common in monogamous birds (Greenwood, 1980; Li & Kokko,

501   2019; Mabry et al., 2013). However, in birds and mammals, sex, mating systems, and parental care

502   are tightly linked, making it difficult to disentangle factors shaping sex differences in exploratory

503   behavior. In the present study, males of all three species tended to be more explorative than

504   females, particularly when translocated longer distances and, therefore, in less familiar

505   environments. Even in *O. sylvatica*, a species where females perform parental care and have wider

506　　space use, males tended to be more explorative after translocations. Male-biased dispersal and
507　　higher male exploration rates have also been observed in some frogs without parental care
508　　(*Engystomops pustulosus*: Lampert et al., 2003; *Bufo bufo*: Ogurtsov et al., 2018; *Xenopus*
509　　*tropicalis*: Videlier et al., 2015). Thus, regardless of parental care strategies, different life histories,
510　　and sex differences in home range size, male amphibians tend to be more exploratory, suggesting
511　　that other factors, such as male-biased dispersal and high intra-sexual male competition may be
512　　associated with the sex difference in exploration.

513

514　　*Linking androgens to exploration and navigation*
515　　Androgens have been linked to spatial abilities in mammals for several decades (Dawson et al.,
516　　1975; Galea et al., 1995; Isgor & Sengelaub, 1998; Joseph et al., 1978; Schulz & Korz, 2010;
517　　Sherry & Hampson, 1997; Stewart et al., 1975; Williams et al., 1990). Clint et al. (2012) proposed
518　　that the often observed male superiority in spatial navigation might be a side effect of sex
519　　difference in androgen levels rather than an adaptation to direct selective pressures on males'
520　　spatial abilities. Our results are somewhat in line with this hypothesis as females did not
521　　outperform males when expected based on adaptive predictions. Additionally, although we did not
522　　observe a correlation between homing success and androgen levels, we found three associations
523　　between androgen levels and spatial behavior.

524

525　　Higher baseline androgen levels predicted more exploration after translocation in *D. tinctorius*,
526　　and the amount of exploration during the navigation task was associated with an increase in
527　　androgen levels in *A. femoralis*. We also found that males, on average, had higher androgen levels
528　　and higher exploration rates despite the variation in the parental sex roles and high inter-individual
529　　variation. Exploration underlies the development of most spatio-cognitive abilities (McNaughton
530　　et al., 2006; O'keefe & Nadel, 1978), including spatial memory, presumably used by poison frogs
531　　for navigation (Beck et al., 2017; Liu et al., 2016, 2019; Pašukonis et al., 2014, 2016, 2019).
532　　Therefore, the association of explorative behavior with androgen levels, especially during the
533　　development of spatial memory, might have cascading effects on sex differences in spatial
534　　behavior and abilities. Quantifying or manipulating androgen levels during ontogeny and learning,
535　　rather than during the spatial task performance, might provide a better understanding of the link
536　　between individual differences in the navigational performance observed in our study and

537   androgen levels. We also found that baseline androgens correlated with homing accuracy in *O.*

538   *sylvatica* in both sexes, further supporting a potential link between androgens and navigational

539   performance. While experimental androgen manipulations are needed to understand the interplay

540   between hormone levels and spatial behavior, our findings lend more support to the androgen

541   spillover hypothesis of sex differences in spatial cognition.

542

543   *Conclusions*

544   We found that parental behavior drives space use patterns but not the navigational performance in

545   poison frogs. Most observed sex differences indicated more developed navigational ability and

546   increased exploratory tendency in males, even in species where females show wider-ranging

547   movement for parental care and mate-seeking. Indeed, most previous literature on sex differences

548   in vertebrate spatial abilities shows either no sex differences or better performance in males. We

549   also found higher average androgen levels in males of all three species despite the marked species

550   differences in parental sex roles and aggressive female behavior. However, there was a high inter-

551   individual variation in androgens and a large overlap between sexes. Some of this inter-individual

552   variation in androgen levels was related to individual differences in exploration and homing

553   accuracy, suggesting an interplay between androgens and spatial behavior. Therefore, our findings

554   are more consistent with the androgen spillover hypothesis than the widely accepted adaptive

555   specialization hypothesis. We speculate that sex differences in spatial abilities could be a

556   byproduct of selective pressures on sexual traits such as aggressiveness and the associated increase

557   in androgen levels. However, the indirect effects of androgens, such as increased male exploration

558   tendency, are likely to be adaptive and maintained in the context of male territoriality and

559   widespread male parental care in poison frogs.

560

561   **Materials and Methods**

562   *Study species*

563   We studied three poison frog species with different life histories and parental sex roles: the

564   Brilliant-Thighed Poison Frog (*Allobates femoralis* [Boulenger 1884], Aromobatidae), the Dyeing

565   Poison Frog (*Dendrobates tinctorius* [Cuvier 1797], Dendrobatidae), and the Diablito Poison Frog

566   (*Oophaga sylvatica* [Funkhouser 1956], Dendrobatidae). *Allobates femorali*s and *D. tinctorius*

567   occur in syntopy in the Guiana Shield, but *A. femoralis* has a wider range across Amazonia (T.

568   Grant et al., 2006). *Oophaga sylvatica* is endemic to the Chocoan Rainforest of the Pacific Coast

569   of Ecuador and Colombia (T. Grant et al., 2006). All three species are diurnal, breed throughout

570   the local rainy season, and shuttle tadpoles from terrestrial clutches in the leaf litter to aquatic

571   tadpole nurseries (T. Grant et al., 2006; Silverstone, 1975, 1976). In *A. femoralis*, groups of up to

572   ~ 20 tadpoles are predominantly transported by territorial males and deposited in terrestrial pools

573   (E. Ringler et al., 2013; Roithmair, 1992). Females take over tadpole transport when males

574   disappear (E. Ringler, Pašukonis, et al., 2015). In *D. tinctorius*, one or two tadpoles are transported

575   by males (but see E. K. Fischer & O'Connell, 2020; Rojas & Pašukonis, 2019 for reports of female

576   transport) to terrestrial and arboreal pools (Fouilloux et al., 2021; Rojas, 2014, 2015; Rojas &

577   Pašukonis, 2019). After tadpole deposition into pools, no further parental care is provided in *A.*

578   *femoralis* and *D. tinctorius*. In contrast, one or two tadpoles of *O. sylvatica* are transported by

579   females and deposited into water-filled plants (Silverstone, 1973; Summers, 1992; Zimmermann

580   & Zimmermann, 1981). Tadpoles feed on unfertilized eggs, which the mother returns to provide

581   every ~ 3 - 7 days (this study and personal observation by E. Tapia communicated to LAC). In all

582   three species, males and females show site fidelity, but the levels of aggressiveness and

583   territoriality vary. In *A. femoralis* and *O. sylvatica*, males vocally advertise and aggressively

584   defend small territories, while females visit males for mating and show no aggressive behavior

585   (M.-T. Fischer et al., 2020; M. Ringler et al., 2009; Roithmair, 1992; Silverstone, 1973; Summers,

586   1992; this study). In *D. tinctorius*, both males and females show intra-sexual aggression as part of

587   territoriality and/or mate guarding, but males do not vocally advertise(Born et al., 2010; Rojas &

588   Pašukonis, 2019; this study).

589

590   *Study sites*

591   Data for *A. femoralis* and *D. tinctorius* were collected over five field seasons between 2016 and

592   2020 in two different plots at the Nouragues Ecological Research Station (4°02' N, 52°41' W) in

593   the Nature Reserve Les Nouragues, French Guiana. One plot consists of ~25 ha of lowland

594   rainforest bordering the Arataï river where both *A. femoralis* and *D. tinctorius* naturally occur. The

595   other plots consist of a 5-ha island in the Arataï river where *A. femoralis* and *D. tinctorius* were

596   absent, but an experimental population of *A. femoralis* was successfully introduced in 2012 (E.

597   Ringler, Mangione, et al., 2015). The island population relies primarily on an array of artificial

598   pools for breeding but otherwise lives under natural conditions (E. Ringler et al., 2018). Data for

599   *O. sylvatica* were collected at two sites in Ecuador: Sapoparque La Florida (0°15' S, 79°02' W) in

600   2017 and Reserva Canandé (0°32' N, 79°13' W) in 2019. The La Florida study area (enclosure site

601   hereafter) consisted of a free-ranging population of *O. sylvatica* introduced and kept in two forest

602   enclosures of ~0.25 ha each inside their natural habitat. The natural breeding pools in the

603   enclosures were supplemented by a high density of small artificial plastic pools and suitable plants.

604   The Reserva Canandé study site (natural site hereafter) consisted of a natural *O. sylvatica*

605   population, relying only on natural pools (water-filled plants). For summarized study site and

606   different dataset information see Annex 6 (Tables S9 and S10)

607

608   *Frog tracking*

609   To quantify frog movements, we used two tracking methods, which have been previously used to

610   track poison frogs: harmonic direction-finding and radio-tracking (for more details see Annex 5).

611   We tagged and tracked 311 frogs, located each frog multiple times a day (see further below), and

612   recorded its position and any observed behavior. All study plots were mapped using precision

613   compasses and laser distance meters, establishing a network of labeled reference points (for

614   method details, see M. Ringler et al., 2016). The digital maps were used with the GIS software

615   ArcPad 10 (ESRI, Redlands, USA) on handheld devices for recording the data in the field.

616   Occasionally, when frogs moved out of the mapped area, we recorded their location by GPS

617   position averaging. All data were collected as GIS spatial points with associated behavioral

618   information, checked point-by-point at least twice, and corrected for errors such as wrong frog

619   identities, duplicates, and impossible locations by one of the experiments. All suspect points where

620   frog identity or location could not be unambiguously confirmed and corrected were removed.

621

622   *Quantification of space use*

623   To quantify space use, we tagged 36 *A. femoralis*, 31 *D. tinctorius*, and 31 *O. sylvatica*, which we

624   localized 6055 times and tracked for periods ranging from <1 to 45 days per individual. A subset

625   of these data was used in previous publications on female space use in *A. femoralis* (M.-T. Fischer

626   et al., 2020) and tadpole transport in *D. tinctorius* (Pašukonis et al., 2019). When a frog lost its tag,

627   we attempted to recapture and retag the individual to continue tracking. Identity was confirmed

628   based on unique dorsal or ventral coloration patterns. We excluded all frogs that were tracked for

629   less than two full days (not including the tagging and tag removal/loss day) without any

630   manipulation and handling (tag checks or retagging, see Annex 5). We also removed short and
631   temporally disconnected tracking periods when the frog was retagged. In the end, we had data to
632   quantify the space use of 29 *A. femoralis* (17 females and 12 males) tracked from 5 to 16 days
633   (median = 14 days) and 26 *D. tinctorius* (11 females and 15 males) tracked for 3 to 45 days (median
634   = 14 days). We tracked 29 *O. sylvatica* (14 females and 15 males) for 7 to 20 days (median = 10
635   days) within enclosures and an additional 37 *O. sylvatica* (20 females and 17 males) for 2 to 8 days
636   (median = 3 days) at the natural site.

637

638   The sampling rate (number of locations per day) varied for different datasets and tracking periods.
639   In particular, movements associated with specific behaviors of interest, such as the tadpole
640   transport, were often sampled at a higher frequency. As the sampling rate influences the spatial
641   parameters, we standardized the data by down-sampling all datasets to match the datasets with the
642   lowest sampling rate (~ 4 points per day). An experienced observer (AP) down sampled the data
643   in a two-step procedure that allowed to maintain the maximum spatial and behavioral information.
644   We first counted the number of points per day and selected the days with more than 2 points above
645   the daily average for the respective dataset. We then removed redundant points while trying to
646   keep the most spatially and temporally distributed points, and points with rare behaviors, such as
647   parental care and mating. In a second step, we automatically down-sampled the remaining dataset
648   to a minimum sampling interval of 60 minutes while retaining intermediate points for long (>20
649   m), fast movements, occurring within shorter than 60 minutes. The resulting dataset had 3 to 7
650   points per day per frog (median = 4).

651

652   For summary of space use variables see Annex 6 (Tables S11 and S12). To quantify the space use,
653   we calculated the daily cumulative distance traveled (daily travel hereafter) for 84 frogs tracked
654   for at least two full days. For 76 frogs tracked for a minimum of seven days, we also quantified
655   the maximum movement extent area (movement extent hereafter) as a minimum convex polygon
656   (MCP) and the home range as 95 % utilization density (UD) contour derived from kernel density
657   estimation (KDE) using the "mcp" and "kernelUD" functions of the "adehabitatHR" R package
658   (Calenge, 2006). The smoothing parameter for the KDE was calculated with a conservative plug-
659   in bandwidth selection method with the "hpi" function of the "ks" R package (Chacón & Duong,
660   2018).

661

662   To quantify the influence of parental and reproductive behaviors on movement, we grouped

663   behaviors into three categories: parental and pool associated behavior (parental behavior

664   hereafter), mating associated behavior (mating behavior hereafter), and "other" when neither

665   parental nor mating behavior was observed. Under parental behavior, we included direct

666   observations of tadpole transport and egg-feeding, as well as all points where the frogs were

667   located within one meter of known breeding pools. Males of *O. sylvatica* were sometimes observed

668   next to breeding pools, but we did not consider that as parental behavior as parental care has not

669   been reported in male *O. sylvatica* nor observed in this study. Under mating behavior, we included

670   direct observations of courting and mating behaviors, as well as all points where the frogs were

671   located within one meter from an opposite-sex individual. We categorized each tracking day as

672   "parental", "mating", or "other" whenever the respective behavior was observed at least once on

673   that day. On the days when both parental and mating behavior occurred (12 out of 84 parental

674   behavior days), we categorized the day as "parental" because parental movements were larger in

675   scale. To evaluate the influence of behavior on movement, we then compared the distance traveled

676   on "parental", "mating", and "other" days.

677

678   Our space use measures represent a snapshot of an animal's long-term movement, and some species

679   were tracked in experimental study plots confined by enclosure or water. Therefore, we further

680   validated our tracking data described above with three supplementary datasets, including short-

681   term tracking of *O. sylvatica* in a natural population and multi-year capture-recapture data in

682   natural populations of *A. femoralis* and *D. tinctorius* (Annex 1).

683

684   *Quantification of navigational performance*

685   To quantify the navigational performance, we carried out translocations and measured homing for

686   64 *A. femoralis* (32 females and 32 males), 67 *D. tinctorius* (35 females and 32 males), and 39 *O.*

687   *sylvatica* (19 females and 20 males). Most frogs were tagged and tracked for at least 24 hours

688   before translocation to establish site fidelity to the tagging areas. We presumed the tagging area to

689   correspond to defended territories or core areas within the home range (collectively termed home

690   areas hereafter). We further confirmed site fidelity by behavioral observations of calling, courtship,

691   and repeated use of shelters. In a few instances, *A. femoralis* were translocated immediately after

692   tagging because the territories were already known from a concurrent study (Rodríguez et al.,
693   2020). We did not translocate frogs transporting tadpoles or continuously moving away from the
694   tagging site. The locations of each frog recorded in the home area before the translocation were
695   used as reference points to establish the correct homeward direction and homing success. We
696   translocated one male and one female simultaneously 50 or 200 meters away from their respective
697   home areas. Frog movements were then tracked for 4 or 6 days for 50-m and 200-m translocation,
698   respectively, or until the frogs returned within ~10 meters from their home areas. Frogs that did
699   not return home within the given time were captured and released back at their home areas. In a
700   few instances, the frogs were tracked for longer than 4 or 6 days, but the trajectories were truncated
701   for the analysis.

702

703   For translocation, each frog was captured and placed in an airtight and opaque container. We chose,
704   measured, and located a release site on the study area map using a portable GIS/GPS device and
705   carried the frogs to the release site. To disorient the frogs, the container was rotated multiple times
706   and never carried in a straight line from the capture to the release site. All frogs were captured and
707   released in the afternoon, and the translocation usually took between 30 to 90 minutes. We
708   translocated one male and one female simultaneously from the same area towards the same
709   direction and attempted to vary the translocation direction between pairs within the landscape
710   constraints of the field site. Most frogs were released by placing the container on the ground for at
711   least 5 minutes and then gently opening the lid allowing the frog to leave. In the case of *A. femoralis*
712   tracked in 2017, frogs were removed from a bag by hand and placed under a flower pot with an
713   opening for an exit. If the frogs did not leave the pot within 30 to 60 min, we lifted the pot by hand.
714   These periods of 30 to 60 min were not included in the analysis.

715

716   We directly observed and mapped the initial movements of each frog for at least 30 min after
717   release. For this, we set up a radial grid with a 3-meter radius at the release site, made of colored
718   strings for visual reference, and mapped the frog movements at approximately 0.3 m precision on
719   a tablet PC running a custom Python (version 2.7.3) script allowing us to record the frog position
720   in relation to the visual reference grid. Following the direct observation, we attempted to locate
721   the frogs approximately every 20 to 60 minutes, although longer sampling gaps occurred due to
722   local terrain and weather constraints.

723

724   For summary of navigation variables see Annex 6 (Tables S11 and S12). To measure the

725   movement strategy and the navigational performance, we quantified (1) homing success, (2)

726   explored area, (3) homing trajectory straightness, (4) homing duration, (5) and angular deviation

727   from the home direction (Annex 2). We assumed that the frog is showing homing behavior (yes/no)

728   if the frog approached at least 70% of the distance from the release site to the home area center,

729   defined as the geometric average of frog positions prior to translocation. To estimate the explored

730   area, we calculated the total area within five meters around the movement trajectory. The value is

731   based on a putative perceptual range of a frog being at least five meters. Trajectory straightness

732   was calculated as the ratio between the straight-line distance from the release site to the end of the

733   homing trajectory and the cumulative distance of the actual homing trajectory. To calculate

734   explored area and trajectory straightness, trajectories were down-sampled to the minimum

735   sampling interval of 15 minutes. The homing duration was calculated as the time from the release

736   of the frog to the moment when the frog crossed a 10-meter buffer drawn around the home area

737   polygon. Night-time (12 hours per night) was excluded from homing duration because none of the

738   study species moves at night. Homing success, explored area, and angular deviation were

739   calculated for all translocated frogs. Trajectory straightness and duration were only estimated for

740   the frogs that successfully returned home. Trajectory straightness and angular deviation could not

741   be estimated for some frogs due to missing data in the trajectory.

742

743   *Quantification of androgen levels*

744   For a subset of the frogs used in navigation experiments, we quantified androgen levels using non-

745   invasive water sampling, following the methodology described elsewhere (Baugh & Gray-

746   Gaillard, 2021; Rodríguez et al., 2022). Androgen levels were quantified once in the morning

747   within 2 days before translocation (baseline hereafter) and again in the morning after the frogs

748   returned home by themselves or were returned by the experimenter. We did not quantify androgen

749   levels for the *A. femoralis* and *D. tinctorius* translocated in 2017. Each frog was placed in 40 mL

750   of distilled water inside a small glass container with a dark cover for 60 minutes at the frog capture

751   location and released immediately after. The water sample was pushed through a C18 cartridge

752   (SPE, Sep-Pak C18 Plus, 360 mg Sorbent, 55 - 105 µm particle size, #WAT020515, Waters corp.,

753   Milford, MA, USA) with a 20 mL sterile syringe. Cartridges were immediately eluted with 4 mL

754 of 98 % EtOH into 5 mL glass vials and were stored at first at 4 C when in the field and then

755 transferred to -20 C until analysis.

756

757 Before the ELISA, 1 mL or 2 mL of the original 4 mL sample was dried down with N2 at 37 C

758 and resuspended with 250 uL of the assay buffer (provided in the kit), and incubated overnight at

759 4 C. Samples were brought to room temperature and shaken at 500 rpm for 1 h prior the assay.

760 Samples were plated in duplicate and assays were performed following the manufacturer's

761 protocol. Plates were read at 405 nm, with correction at 570 nm, using a microplate reader

762 (Synergy H1, BioTek Instruments, Winooski, VT, USA) and the concentration of androgens was

763 calculated using the software Gen5 (version 3.05, BioTek Instruments, Winooski, VT, USA). The

764 detection limit for the assay was 7.8 and 2000 pg mL-1 and samples that fell out of this range were

765 removed from the analysis. The cross-reactivity of the testosterone antibody with other androgens

766 is below 15% according to the manufacturer's manual. Samples with the average intra-assay

767 coefficient of variation (CV) above 15% were excluded from the analysis and the resulting average

768 CV was 5.7%. The average inter-assay CV was 7% for five out of nine assays and not available

769 for the other four due to experimenter error. The final reported concentrations were adjusted for

770 the sample volume taken (1 or 2 mL) and sample concentration during drying-resuspending.

771

772 *Weather variables*

773 We measured the understory ambient temperature with temperature-data loggers (HOBO U23 Pro

774 v2, Onset Computer Corp, Bourne, USA) placed ~30 cm above ground and recording temperature

775 at 15 or 30-minute intervals. Because our study species are exclusively diurnal, we measured

776 daytime temperature by averaging all measures from sunrise to sunset. At the *O. sylvatica*

777 enclosure site, we manually measured temperature three times per day at the start, middle, and end

778 of each tracking session with a handheld electronic thermometer (GFTH 95, GHM Messtechnik,

779 Regenstauf, Germany) held slightly above the ground. We averaged the three measurements to

780 obtain daytime temperature. We also calculated mean daytime temperatures for each frog during

781 the navigation experiments by averaging daytime temperatures over the tracking period of each

782 frog (also see Annex 6 Table S12). We did not use the rainfall data because they were strongly

783 correlated with daytime temperature and missing for some tracking periods.

784

Data analyses

All statistics were generated in R Studio (version 1.0.153, RStudio Team, 2020) running R (version 3.6.3, R Core Team, 2020). Space-use plots were generated in QGIS (version 2.14, QGIS.org, 2022), box plots, trajectory plots, and bar plots with ggplot2 R package (Wickham, 2016), circular plots with circular R package (Agostinelli & Lund, 2022), model plots with sjPlot R package (Lüdecke, 2021). Schematic representations and further editing were done with Adobe Illustrator (version 25.2.3, Adobe Inc., Mountain View, CA, USA), and Microsoft PowerPoint (version 16.54, Microsoft Corp., Redmont, WA, USA). All variables and statistical models are summarized in Annex 6 (Tables S11, S12, S13)

Space use

Spatial variables (daily travel, movement extent, home range, and explored area) approximately followed a log-normal distribution and thus we transformed the raw data by natural logarithm to fit the model assumptions. To investigate the sex differences in movement extent and home range, we fitted two linear models (LMs) with movement extent and home range as responses in each model respectively, and sex, species, and their interaction as predictors. As there was a strong interaction between species and sex for both models, we fitted a separate LM for each species with sex as the predictor. As movement extent and home range often correlate with tracking duration, we included the number of days tracked as a covariate. To investigate the influence of behavior and sex on the daily movement, we fitted linear mixed-effects models (LMMs) with daily travel as the response variable using the "lmer" function within the lme4 R package (Bates et al., 2015). We first fitted an LMM for each species with sex, behavior, and daytime temperature as fixed factors and frog identity and tracking date as random factors. We checked for a correlation between daily travel and number of points per day for each species (significant for *D. tinctorius* and *O. sylvatica*, but not for *A. femoralis*) and used number of points per day as a covariate in LMMs when the correlation was significant. For model selection we followed an information-theoretic approach (Burnham & Anderson, 2002) based on the Corrected Akaike's Information Criterion (AICc). We calculated models with all combinations of fixed factors (behavior, sex, daytime temperature) while keeping random factors (id and date) and the covariate (number of points per day). We selected the best single model using the "model.sel" function within the MuMIn R package (Bartón & Barton, 2020). Because parental behaviors mostly occurred in one sex, we also

816   analyzed the influence of behavior on movement for each sex separately. We fitted separate LMMs

817   for each sex of each species with behavior as a fixed factor, (factor with 2 or 3 levels: parental,

818   mating, and other as appropriate for each species and sex), and frog identity and tracking date as

819   random factors. The daytime temperature was only included as a fixed factor if the best model

820   based on AICc included temperature (it did for *A. femoralis*, but not for *D. tinctorius* and *O.*

821   *sylvatica*). We used least-squares means contrasts to compare daily travel between behavioral

822   categories. Post hoc comparisons were done with the "emmeans" function within the emmeans R

823   package (Lenth, 2022) with P-values adjusted by Tukey's method for multiple comparisons

824   (Tukey, 1977).

825

826   *Navigational performance*

827   As species and frogs translocated to different distances showed qualitatively very different

828   movement and homing patterns, we fitted separate models per species and per translocation

829   distance. To investigate the sex differences in the homing success we fitted generalized linear

830   models (GLMs) with binomial error distribution and Logit link function using the "glm" function

831   within R package stats (R Core Team 2020). We used the homing success as a binary response

832   variable with sex, frog weight (except for *O. sylvatica*), and the mean daytime temperature during

833   the entire tracking period as predictors. To investigate sex differences in exploration, we fitted an

834   LM with the natural log-transformed explored area as the response variable and sex, mean daytime

835   temperature, and frog weight as predictors. To investigate sex differences in homing trajectory

836   straightness we fitted a beta regression model for proportions via maximum likelihood using the

837   "betareg" function within the R package betareg (Cribari-Neto & Zeileis, 2010). We used

838   straightness (ratio between 0 and 1) as the response variable with sex and mean daytime

839   temperature as predictors. To investigate sex difference in homing duration we fitted an LM with

840   natural log-transformed homing duration as the response variable and sex, mean daytime

841   temperature, and frog weight as predictors.

842

843   *Androgen levels and navigation*

844   To investigate the relationship between androgens, sex, and movement, we fitted a series of

845   separate models for each species. We first fitted LMMs with log-transformed androgen levels as

846   the response variable, sex, and time point (two-level factor: baseline or back home) as fixed factors,

847   and frog identity as a random factor. For all three species, there was no interaction between sex

848   and sampling time point, and the interaction factor was excluded. To investigate the relationship

849   between baseline androgens and spatial behavior during navigation, we first fitted an LM for each

850   species with the log-transformed explored area as the response variable and baseline androgen

851   levels, sex, translocation distance, homing success, mean daytime temperature, and frog weight as

852   predictors. For successfully homing frogs, we also fitted two GLMs (Gamma distribution, inverse

853   link function) with trajectory straightness and homing duration as response variables and baseline

854   androgen levels, sex, translocation distance, mean ambient temperature, and frog weight as

855   predictors. To be able to evaluate the relative influence of different fixed factors on the response

856   variables, we standardized all continuous predictors by centering and scaling using the "stdize"

857   function from the MuMIn R package. We did not include sex for GLMs of trajectory straightness

858   and homing duration of *A. femoralis* because androgen levels were available for only one homing

859   female. If movement itself had an influence on androgen levels, we expected the amount of

860   exploration to have a significant influence on androgen levels after the navigation task. Therefore,

861   we calculated delta androgen levels by subtracting the baseline from the back home levels and

862   fitted an LM with delta androgen levels as a response variable and the explored area, sex, tracking

863   duration, homing success, mean daytime temperature, and frog weight as fixed factors. To reduce

864   the number of covariates, for each model mentioned above, we compared the full models against

865   a model without the mean temperature or the frog weight using the "drop1" function of the stats R

866   package. We removed mean temperature and frog weight from the final model if the model

867   excluding these factors (separately) was not significantly different ($P > 0.1$).

868

869   *Ethics statement and permits*

870   We strictly adhered to the current US, French, Ecuador, and European Union law, and followed

871   the 'Guidelines for use of live amphibians and reptiles in the field and laboratory research' by the

872   Herpetological Animal Care and Use Committee (HACC) of the American Society of

873   Ichthyologists and Herpetologists (Beaupre et al., 2004); and the Association's for the Study of

874   Animal Behaviour (ASAB) 'Guidelines for the use of live animals in teaching and research'

875   (ASAB, 2020). The research was approved by the Institutional Animal Care and Use Committee

876   of Stanford University (protocol ID 33211, issued to LAO) and by the Animal Ethics and

877   Experimentation Board of the Faculty of Life Sciences, University of Vienna (approvals No 2016-

878 002, 2016-003, 2018-10, issued to AP). The permits in French Guiana were issued by the local

879 authorities (DIREN premits: R03-2016-10-21-002, N°2015-289-0021, n°2011-

880 44/DEAL/SMNBSP', issued to ER). In addition to these permits, all protocols for fieldwork were

881 approved by the scientific committee of the Nouragues Ecological Research Station (approval

882 communicated to AP) and the Nouragues Nature Reserve (partnership agreement No 01-2019 with

883 AP, BR, ER, MR). The permits in Ecuador were issued by the local authorities (Ministerio de

884 Ambiente, approval document No 013-18-IC-FAU-DNB/MA, issued to LAC). In addition, the

885 authorization to work in Reserva Canandé was given by reserve authority Fundación Jocotoco,

886 Ecuador (approval communicated to AP).

887

Data availability

889 All data and associated scripts will be made available after publication.

890

902

919

Competing interests

921   Authors declare no competing interests.

922

Author contributions

924   AP: Conceptualization (lead), methodology (lead), investigation-field (lead), investigation-
925   laboratory (lead), data curation (lead), formal analysis (lead), data visualization (lead), writing-
926   original draft (lead), funding acquisition (lead), permit acquisition (lead), other resources (lead),
927   supervision (lead).
928   SJSR: Investigation-field (lead), data curation (supporting), formal analysis (supporting),
929   writing-review & editing (supporting).
930   MTF: Investigation-field (supporting), data curation (supporting), writing-review & editing
931   (supporting).
932   MCL: Methodology (supporting), investigation-field (supporting), formal analysis (supporting),
933   funding acquisition (supporting), writing-review & editing (supporting).
934   DAS: Investigation-field (supporting), data curation (supporting), writing-review & editing
935   (supporting).
936   BR: Methodology (supporting), investigation-field (supporting), data curation (supporting),
937   funding acquisition (supporting), writing-review & editing (supporting).
938   MR: Methodology (supporting), investigation-field (supporting), data curation (supporting),
939   writing-review & editing (supporting), other resources (supporting).
940   ABR: Investigation-field (supporting), writing-review & editing (supporting).
941   AML: Investigation-field (supporting), writing-review & editing (supporting).
942   ER: Writing-review & editing (supporting), funding acquisition (supporting), permit acquisition
943   (lead), other resources (supporting), supervision (supporting).
944   CR: Methodology (supporting), investigation-laboratory (supporting), formal analysis
945   (supporting), writing-review & editing (supporting).
946   LAC: Writing-review & editing (supporting), permit acquisition (lead), other resources
947   (supporting).

948   LAO: Conceptualization (lead), methodology (supporting), data visualization (supporting),
949   writing-original draft (supporting), writing-review & editing (supporting), funding acquisition
950   (lead), permit acquisition (lead), other resources (lead), supervision (lead).
951

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