Sex-specific determinants of fitness in a social mammal

Sophie Lardy, Dominique Allainé, Christophe Bonenfant and Aurélie Cohas

Appendix C – Effect of group size and composition on individual lambda

The way ecologists should measure fitness in the wild remains controversial (Grafen, 1988; Blomquist, 2009). Discussions arise whether rate sensitive measures of fitness such as individual lambda (λ_i , McGraw and Caswell, 1996) or individual contribution to population growth rate (Coulson et al., 2006) should be preferred over cruder measures of fitness like lifetime reproductive success (LRS, Clutton-Brock, 1988). Fitness is related to the rate of spread of a gene in the population (Charlesworth, 1994) and both theoretical (Benton and Grant, 2000) and empirical (Brommer et al., 2004) studies suggest that, in some instances, LRS could be a better proxy of fitness than λ_i in evolutionary studies of natural populations. Although there is a strong analytic link between these two measures (McGraw and Caswell, 1996), reproductive events occurring at later ages are downweighted compared to early events when using λ_i (Fig. C1). To the contrary, LRS weight all reproductive events the same, irrespective of its timing in an individual's life. As shown by Brommer (2004), this major difference is likely to lead to a better correlation between LRS and fitness in Alpine marmots because the fitness payoff from offspring produced late in life is likely to be too strongly de-emphasized by λ_i (Fig. C1) due to the slow pace of life of this species and the stable dynamic of the population studied (Farand et al., 2002). However, because no definitive answer has been reached yet, we replicated our analyses using λ_i (McGraw and Caswell, 1996) in addition to the LRS. Individual λ is the dominant eigenvalue of an individual-based Leslie matrix where the number of offspring produced by an individual at a given reproductive event corresponds to the number of pups produced (>one), confirmed by genetic analyses surviving to the age of one, divided by two (McGraw and Caswell, 1996).

Fig. C1. Correlation between the individual lambda (λ_i) and the lifetime reproductive success (LRS) for dominant male (N = 52) (a) and female (N = 39) (b) Alpine marmots monitored in the Grande Sassière nature reserve (French Alps) between 1990 and 2010.



Males' and females' λ_i

 λ_i and LRS have a curvilinear relationship, where the increase in λ_i with LRS levels off rapidly (Fig. C1).

As for LRS, the range of λ_i was similar for the two sexes ([0, 1.48], $n_{males} = 52$, $n_{females} = 39$). Neither the median λ_i ($\tilde{x}_{males} = 1.13$, $\tilde{x}_{females} = 1.17$, W = 943.5, P = 0.57) nor the variance ($\sigma^2_{males} = 0.18$, $\sigma^2_{females} = 0.12$, F = 1.55, P = 0.16) of λ_i differed between sexes (Fig. C2).

Individual λ variations mainly resulted from the variations in tenure length (21.83% and 22.59% in males and females, respectively) and pup survival (63.62% and 53.33%) in both sexes. The contribution of breeding rate to the observed variations in λ_i was lower in males than in females (8.61% versus 20.90%). Finally, the average number of pups produced had the lowest contribution in both males (5.94%) and females (3.18%). Contributions to both λ_i and LRS were highly similar, except from the greater contribution of pup survival than

Fig. C2. Distribution of individual lambda (λ_i) in dominant male (N = 52) (a) and female (N = 39) (b) Alpine marmots monitored in the Grande Sassière nature reserve (French Alps) between 1990 and 2010.



of tenure length to λ_i variations.

Group size effects on λ_i of males and females

We found different effects of group size on λ_i and LRS of male and female Alpine marmots. As for LRS, the relationship between the average group size and λ_i was different for males and females ($\chi^2 = 10.5$, df = 2, P = 0.05). Fitness of males as measured by λ_i increased until an average group size of 5.53 and decreased thereafter (Fig. C3). For females, λ_i showed a non-significant linear increase with group size (Table C1).

Group composition and instability effects on λ_i of males and females

As for LRS, group composition did not have the same impact on males' and females' λ_i (Table C2). The effects of the average number of same-sex subordinates in the group on males' and females' λ_i and LRS were similar, also a stronger effect was evidenced on males Fig. C3. Effects of the average group size on individual lambda (λ_i) in dominant male (N = 52) (a) and female (N = 39) (b) Alpine marmots monitored in the Grande Sassière nature reserve (French Alps) between 1990 and 2010. The dots represent the observed data, their size being proportional to the sample size and the numbers in brackets indicate the sample size. The lines represent the model predictions (plain) and its associated standard error (dotted).



than on females λ_i ($\chi^2 = 17.3$, df = 2, P > 0.001). Both males' and females' λ_i increased, respectively, until an average of 2.44 and 1.88 subordinates of the same sex in the group and then decreased (Fig. C4). The average number of same sex subordinates contributed to 93.14% and 36.18% of the observed variation in the λ_i of males and females. As for LRS, the average number of other sex subordinates had a negative effect on males' λ_i (Table C2), but no effect on females' λ_i . As for LRS, the average number of the other sex subordinates contributed only little to male's and females' λ_i (6.74% and 6.89%). If males' and females' LRS decreased with the average number of partner changes encountered during the dominant tenure, only females' λ_i significantly decreased with partner changes. Fig. C4. Effects of the average number of same sex subordinates on the individual lambda (λ_i) of dominant male (N = 52) (a) and female (N = 39) (b) Alpine marmots monitored in the Grande Sassière nature reserve (French Alps) between 1990 and 2010. The residual λ_i has been obtained after correction for the effect of the average number of other sex subordinates in males and of group instability in females. The dots represent the observed data, their size being proportional to the sample size and the numbers in brackets indicate the sample size. The lines represent the model predictions (plain) and its associated standard error (dotted).



Concluding remarks comparing λ_i and LRS

Contrary to LRS, we found evidence for an optimal group size on fitness in males but not in females. However, the optimal group composition for fitness holds for both sexes. Fitness of male and female marmots estimated from λ_i reached a maximum for an intermediate average number of same sex subordinates. Our results also showed that tenure length and offspring survival are the two components contributing the most to the individual variation in λ_i . However, tenure length appeared to be a much weaker determinant of λ_i than of LRS. These results can be explained by the fact that λ_i gives a disproportionate weight to early reproduction and strongly de-emphasizes the fitness payoff from offspring produced late in life and because the variability of λ_i is reduced compared to the variability of LRS (Brommer et al., 2004). In Alpine marmots, virtually all individuals first reproduce at three years of age (94% of males and 97% of females), while longevity is highly variable ranging from 3 to 16 years. Consequently, although the results obtained with λ_i and LRS support our prediction of sex-specific optimal group characteristics for fitness, λ_i may not be the most appropriate proxy of individual fitness in this species.

				Males				Fem	ales	
Model terms	Errors	Links	$\beta \pm SE$	2	P-value	Я	$\beta \pm SE$	2	P-value	Я
Av. group size	Normal	Gaussian	$0.71 {\pm} 0.21$	3.45	< 0.01	010	0.02 ± 0.04	0.46	0.65	
Av. group size ²			-0.06 ± 0.02	-3.13	< 0.01	0.49	I	ı	I	I

Table C1. Effect of the average group size on individual lambda $(\lambda_{(i)})$ in male (N = 52) and female (N = 39) Alpine marmots followed in the Grande Sassière nature reserve (French Alps) between 1990 and 2010.

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Table C2. Effect of group composition and instability	Alpine marmots followed in the Grande Sassière natur

	В		rrelation				
	% variance ^a	36.18		6.89	56.92	variable, R: Co	
Females	P-value	0.02	0.04	0.49	0.02	explanatory	
	N	2.50	-2.18	0.70	-2.36	r by the	
	$\beta \pm SE$	$0.47 {\pm} 0.19$	-0.15 ± 0.07	0.03 ± 0.05	-0.52 ± 0.22	in accounted for	
	Я		0.58				
	$\% \text{ variance}^a$	09 14	90.14	6.74	0.12	% of explained	
Males	P-value	<0.01	<0.01	0.02	0.62	d error, a :	
	~	4.42	-3.43	-2.30	-0.50	: standar	
	$\beta \pm SE$	$0.68{\pm}0.15$	-0.1 4±0.04	-0.16 ± 0.07	-0.17 ± 0.33	parameters, SE	
	Links	log				Stimated	
	Errors	Neg. Bin.				in bold. β : E	
	Model terms	$\lambda_{(i)}$ Av. same sex sub.	Av. same sex $sub.^2$	Av. other sex sub.	Av. partner changes	The significant variables are	

coefficient between the observed data and the values predicted by the model containing only the significant variable. Abbreviations: Neg. Bin. : Negative binomial, Av.: Average number of.

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