

Plasticity in sexual size dimorphism and Rensch's rule in Mediterranean blennies (Blenniidae)

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Abstract: Comparative analyses of sexual size dimorphism (SSD) across species have led to the discovery of Rensch's rule. This rule states that SSD increases with body size when males are the largest sex, but decreases with increasing size when females are larger. Within-species comparisons of SSD in fish are rare, yet these may be a valuable tool to investigate evolutionary patterns on a fine scale. This study compares SSD among closely related populations of three species of Mediterranean blennies (Blenniidae): *Microlipophrys canevae* (Vinciguerra, 1880), *Parablennius incognitus* (Bath 1968), and *Aidablennius sphyinx* (Valenciennes, 1836). SSD varied more among populations than among species and Rensch's rule was confirmed within two species. It is not likely that the variation among populations in SSD mirrors genetic variation, as many of the populations were in close proximity of one another, with a high potential for genetic exchange. This study complements larger scale analyses of other taxa and demonstrates the fine scale on which evolutionary processes responsible for Rensch's rule may be operating.

Résumé : Des analyses comparatives du dimorphisme sexuel de la taille (SSD) chez les différentes espèces ont abouti à la formulation de la loi de Rensch. Cette loi indique que le SSD augmente en fonction de la taille corporelle lorsque les mâles représentent le groupe de plus grande taille, mais qu'il décroît en fonction de la taille lorsque les femelles sont plus grandes. Les comparaisons du SSD à l'intérieur d'espèces de poissons sont rares, bien qu'elles puissent être un outil précieux pour étudier les patrons d'évolution à une échelle fine. Notre étude compare le SSD chez des populations fortement apparentées de trois espèces de blennies (Blenniidae) méditerranéennes : *Microlipophrys canevae* (Vinciguerra, 1880), *Parablennius incognitus* (Bath 1968), and *Aidablennius sphyinx* (Valenciennes, 1836). Le SSD varie plus entre les populations qu'entre les espèces et la loi de Rensch s'applique au sein de deux des espèces. Il est peu vraisemblable que la variation du SSD dans les populations reflète une variation génétique car plusieurs des populations vivent à peu de distance les unes des autres, avec un fort potentiel d'échanges génétiques. Notre étude vient compléter d'autres analyses à plus grande échelle sur d'autres taxons et elle démontre à quelle échelle fine peuvent opérer les processus évolutifs responsables de la loi de Rensch.

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Introduction

Comparative analyses of sexual size dimorphism (SSD) have led to the discovery and confirmation of a broad macroecological pattern termed Rensch's rule (Rensch 1950). This rule states that in comparisons among species, SSD increases with body size when males are larger than females, whereas size dimorphism decreases with increasing body

size when females are larger. Rensch's rule has been demonstrated in comparative studies of insects, reptiles, birds, and mammals (Fairbairn 1997; Colwell 2000; Kratochvil and Frynta 2002; Székely et al. 2004; Johansson et al. 2005; Blanckenhorn et al. 2006, 2007; Raihani et al. 2006), but appears to be more consistent in taxa with male-biased SSD than in taxa with female-biased SSD (Webb and Freckleton 2007).

Various functional hypotheses have been proposed to explain Rensch's rule (reviewed by Fairbairn 1997). One of the mechanisms receiving most support is the correlated response of females to sexual selection on males. If there is stronger selection for males to grow larger, female size may, to some degree, follow owing to a lack of sex-biased genetic variance (Badyaev 2002). However, since selection is stronger on males, male size should respond more to the apparent selective forces than female size and therefore SSD increases with body size. Within this hypothesis, female-biased SSD increases with decreasing body size when there is strong sexual selection for smaller males, for instance when agility in courtship displays is important for reproductive success (Székely et al. 2004). Another hypothesis predicts that Rensch's rule occurs through an effect of resource availability, which acts on both body size and SSD.

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It assumes that resource-limited environments favour smaller body sizes in both males and females and that resource limitation also has a detrimental effect on any investments by males in secondary sex traits, including body size (Colwell 2000). Therefore, under resource limitation, both overall body size and a sexual difference in body size should decrease.

More recently, the differential-plasticity hypothesis was introduced by Fairbairn (2005) and was used to explain intraspecific variation in SSD among laboratory-reared water striders (*Aquarius remigis* (Say, 1832)). In this hypothesis, Rensch's rule is explained by greater phenotypic plasticity in males than in females. When, for instance, adult body size is positively affected by rearing temperature, the response in male body size can be stronger than in female size, through which SSD will increase with increasing body size under the influence of higher rearing temperatures.

Fairbairn (2005) investigated intraspecific variation in SSD, whereas most studies that find support for a correlated response to sexual selection have used interspecific comparisons. The level at which comparisons are made may have an influence on which mechanisms are revealed. A response to different sexual selection mechanisms may typically appear in multiple species comparisons, where for instance different mating systems can occur within the comparison. By contrast, comparisons among populations may typically reveal a response to environmental factors, such as the availability resources or rearing temperature, reflecting the different environments in which the populations live.

Given the known extreme variability in SSD among fishes (Parker 1992), this taxon is surprisingly underrepresented in comparative studies of SSD and Rensch's rule. Two exceptions are recent studies on salmonids (Young 2005) and on a cyprinid species (Pyron et al. 2007). Young (2005) could not confirm Rensch's rule in a multiple species comparison but did confirm the rule among populations within species. In addition, this comparison among populations revealed that SSD varied to the same extent among populations as it did among species. Pyron et al. (2007) showed that SSD among populations followed Rensch's rule and ranged from male-biased to female-biased within one cyprinid species. Applying such fine-scaled analysis to highly plastic organisms such as fishes may offer a powerful way of detecting evolutionary patterns and deducing their underlying causes. This may be a valuable complement to broad-scale comparisons among species or higher taxa, which usually differ from one another in many more ways than do populations of the same species.

Mediterranean blennies (Blenniidae) provide a good system for comparative studies of closely related populations. Various blenny species are widely distributed along the Mediterranean coastline (Zander 1972), with populations isolated by stretches of unsuitable habitats such as sandy beaches. In addition, blennies are highly sexually dimorphic in size, with males usually being larger than females, although variation in SSD occurs among species. The blenny mating system is highly promiscuous and characterized by male uniparental care, i.e., males care for the eggs spawned by females in a natural hole in the substratum. Body size plays a crucial role in competition for nest sites and matings (Almada et al. 1994; Locatello and Neat 2005). Adult blen-

nies are not known to migrate, but it is likely that the larvae, which have a pelagic phase of variable length after hatching (e.g., 29 days for the shanny (*Lipophrys pholis* (L., 1758))); Francisco et al. 2006), can disperse over relatively large distances. Localized populations of *L. pholis* from across the entire Portuguese coast were not significantly genetically differentiated (Francisco et al. 2006).

In this study, we used three species of Mediterranean blennies in a fine-scaled comparison of taxa to investigate variation in the degree of SSD among closely situated populations. These comparisons enabled tests of whether Rensch's rule applies within these species.

Materials and methods

Between April and June 2005, we sampled populations of three blenny species (Blenniidae) at 22 coastal locations on the Costa Brava in Spain and the Côte d'Azur in France (Table 1). These two main sampling areas were more than 330 km apart in a straight-line distance (the distance along the coastline would have been much longer, i.e., more than 500 km), and covered a 60 km stretch of coast in Spain and 52 km in France. In Spain we sampled 12 populations, with the two closest sites being 0.6 km apart; in France we sampled 10 populations, with the closest two populations being 0.3 km apart. We sampled stretches of rocky coastline in bays, usually separated by stretches of sandy beach or large distances of coastline. All three blenny species were breeding throughout the study period.

The three study species were *Microlipophrys caneavae* (Vinciguerra, 1880), *Parablennius incognitus* (Bath 1968), and *Aidablennius sphyinx* (Valenciennes, 1836). Adults of all three species are sexually dimorphic in size and nuptial colouration, and *A. sphyinx* and *P. incognitus* also have clear sexual dimorphism in body shape (i.e., males have larger dorsal fins and larger cirri than females). Our three focal species exhibit life histories that are common in the family Blenniidae, including a pelagic larval phase. *Microlipophrys caneavae* and *P. incognitus* both occurred at 21 of our 22 study sites, and *A. sphyinx* occurred at 17 sites.

Body size measurements

At each study site, we caught blennies with small hand nets while snorkelling. The blennies' clearly visible secondary sex traits (colouration, ornamentation, external glands) are mostly absent in juveniles, which allowed for an easy distinction between adults and juveniles. Only adults were included in this study. We used clove oil at a concentration of approximately 3 drops/L of seawater to anaesthetize the fish before measuring standard length (L_s) to the nearest millimetre with a fine-scale ruler. The fish were not handled out of the water for more than 20–30 s, and were then placed in a bucket of fresh seawater to recover (which took no longer than 10 min). At each site, we attempted to catch a minimum of 10 adult individuals of each sex of each species. To prevent capturing and measuring the same individuals more than once, we kept all fish of one specific sex and species in a large bucket (10 L) until we reached our target sample size. When our target sample size was reached, the recovered fish were released near their point of capture.

Table 1. Locations for each of the 22 sample sites in this study.

Locality	Name	Coordinates
Spain		
1	Aiguafreda	41°57.858'N, 3°13.664'E
2	L'Estartit	42°03.190'N, 3°12.514'E
3	Port de la Selva	42°20.606'N, 3°12.072'E
4	Pals	41°58.717'N, 3°12.596'E
5	L'Escala	42°07.872'N, 3°07.414'E
6	Montgó	42°06.490'N, 3°10.270'E
7	Port de la Vall	42°20.563'N, 3°11.254'E
8	Banyuls	42°28.996'N, 3°07.803'E
9	Roses	42°14.735'N, 3°10.935'E
10	Roses II	42°14.243'N, 3°12.481'E
11	Sa Tuna	41°57.660'N, 3°13.801'E
12	Sa Riera	41°58.436'N, 3°12.619'E
France		
13	Saint-Clair	43°08.381'N, 6°22.892'E
14	Pointe du Layet	43°08.827'N, 6°25.283'E
15	Port du Niel	43°02.069'N, 6°07.616'E
16	Les Oursinières	43°05.219'N, 6°01.274'E
17	Cap Brun	43°06.311'N, 5°58.265'E
18	Les Bonettes	43°05.905'N, 6°01.000'E
19	Giens	43°02.095'N, 6°07.821'E
20	Beau Rouge	43°04.736'N, 6°02.375'E
21	Pointe du Gaou	43°04.127'N, 5°47.682'E
22	Le Pin de Galle	43°06.237'N, 6°00.292'E

Analyses

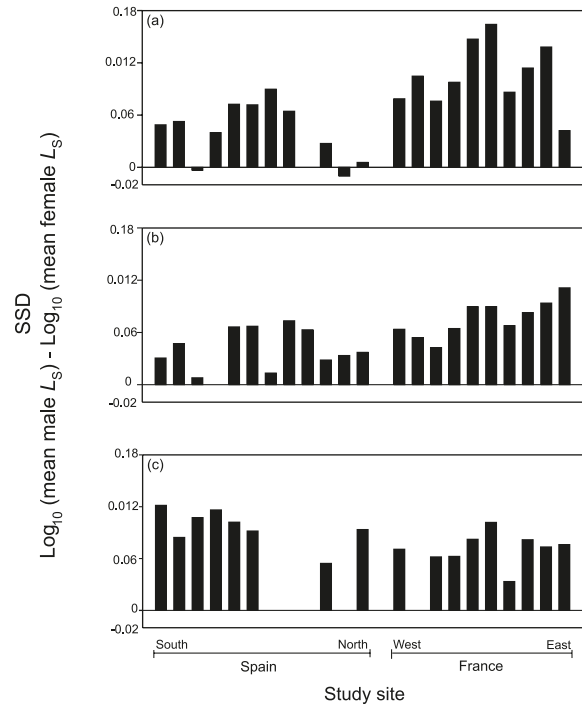
As a measure of SSD for each study site, we used the widely accepted index $\text{Log}_{10}(\text{mean male } L_s) - \text{Log}_{10}(\text{mean female } L_s)$ (Smith 1999). In this paper, SSD generally refers to our index based on the mean male and mean female body sizes of each population. However, when considering differences among species in SSD, we generated “species mean SSD” by calculating SSD at each site, and then averaging across all sites for each species. We did not reach our target sample size of 10 males and 10 females for *M. canevae* at four of the study sites. However, analyses with and without these four sites yielded similar results, therefore we present the results with these sites included.

To test for an allometric relationship between male and female body size, and to determine the slope of the regression line, we used ordinary least-square (OLS) regression analyses. Many authors use model II regressions (i.e., major axis (MA) or reduced major axis (RMA)), although the appropriateness of these methods when testing for Rensch’s rule is arguable (Smith 1999). Webb and Freckleton (2007) used a SIMEX approach (simulation–extrapolation; Cook and Stefanski 1994) to show that the OLS estimate of the slope is at least as good an estimate of the slope of $\text{Log}_{10}(\text{female})$ size on $\text{Log}_{10}(\text{male})$ size as are model II regressions, even with the apparent measurement error in the independent variable. Exploratory analyses using SIMEX gave similar results for the data used in this study, confirming that OLS estimates were appropriate.

Ethical note

A total of 1911 blennies of the three species were caught,

Fig. 1. The extent of sexual size dimorphism for (a) *Microlipophrys canevae*, (b) *Parablennius incognitus*, and (c) *Aidablennius sphyinx* at 22 study sites across the Mediterranean coasts of Spain and France. The study sites are ordered from southernmost to northernmost for Spain, and westernmost to easternmost for France.



anaesthetized, measured, and released in a manner that conformed to the guidelines of the Association for the Study of Animal Behaviour. The fish were not exposed to the anaesthetic for more than 5 min or handled outside of water for longer than 20–30 s. On one occasion, 25 fish died. The cause of this mortality was unknown and such an event did not recur. This work was approved by the University of East Anglia’s Animal Ethics Committee.

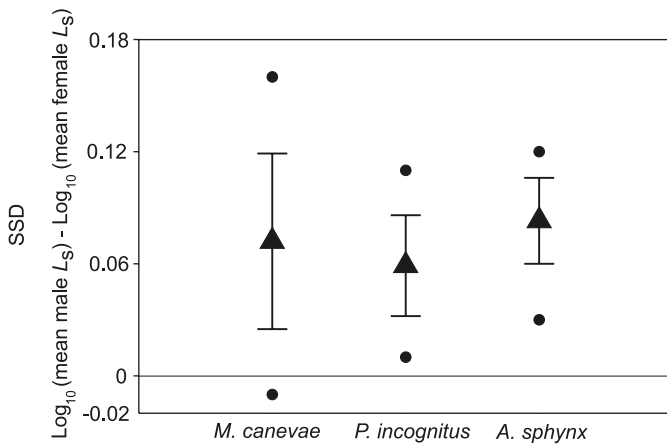
Results

Variation in SSD among populations and species

The extent of SSD varied substantially among study sites for all three species (Fig. 1). The most extensive variation was observed in *M. canevae*, where SSD ranged from males being slightly smaller (2%) than females to males being nearly 1.5 times (46% larger than) the size of females. Males of *M. canevae* were smaller than females in 2 of 21 populations. In the other two focal species, only male-biased SSD was recorded; male *P. incognitus* were 2%–29% larger than female *P. incognitus* and male *A. sphyinx* were 8%–32% larger than female *A. sphyinx*.

The extent of variation in SSD among populations exceeded the variation among species (Fig. 2). In *M. canevae*, the maximum difference in SSD between populations was 6.8 times larger than the maximum difference in SSD between species (i.e., difference in species mean SSD between *P. incognitus* and *A. sphyinx*; Fig. 2). For *P. incognitus* and *A. sphyinx*, maximum interpopulation differences were 4 times and 3.6 times larger, respectively, than the maximum difference in SSD among species. There were no sig-

Fig. 2. Species mean sexual size dimorphism (SSD; \blacktriangle) for three Mediterranean blenny species (*Microlipophrys canevae*, *Parablennius incognitus*, and *Aidablennius sphyinx*). The circles represent the minimum and maximum population mean SSDs observed for each species. Error bars are ± 1 SD.



nificant differences in species mean SSDs between any of the three blenny species (ANOVA: $F_{[2,56]} = 2.42$, $P = 0.1$; post hoc Tukey's tests: *M. canevae* vs. *P. incognitus*, $P = 0.43$; *M. canevae* vs. *A. sphyinx*, $P = 0.58$; *P. incognitus* vs. *A. sphyinx*, $P = 0.08$).

Rensch's rule among populations

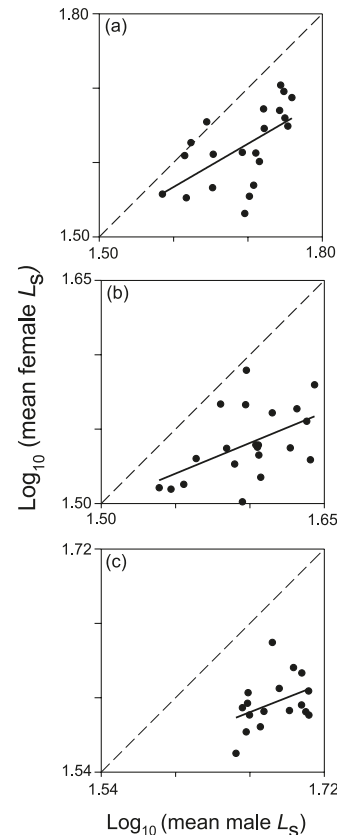
The slopes of the regression lines of mean female size regressed on mean male size were < 1 in all three species (Fig. 3), confirming that Rensch's rule occurred among the sampled populations within each species. For *M. canevae*, mean male and female size were significantly related ($R^2 = 0.35$, $F_{[1,19]} = 10.43$, $P = 0.004$; Fig. 3a) and the regression line had a slope of 0.58. The 95% confidence interval for the slope was 0.21–0.96 and thus differed significantly from 1 ($P < 0.05$). For *P. incognitus*, the relationship between mean male and female size ($R^2 = 0.26$, $F_{[1,19]} = 6.55$, $P = 0.019$; Fig. 3b) had a slope of 0.41 and also differed significantly from 1 (99% confidence interval = -0.05 to 0.87 , $P < 0.01$). For *A. sphyinx*, the relationship between mean male and female size was not significant ($R^2 = 0.16$, $F_{[1,15]} = 2.85$, $P = 0.11$; Fig. 3c), but its slope of 0.39 differed statistically from 1 (95% confidence interval = -0.10 to 0.89 , $P < 0.05$).

Discussion

SSD in the three examined blenny species varied substantially more among populations within each species than among species. One species, *M. canevae*, displayed the full range of SSD, from slightly female-biased to extremely male-biased. SSD in *A. sphyinx* and *P. incognitus* was consistently male-biased but also varied substantially among populations. By contrast, species mean SSDs were similar across species. Ultimately, Rensch's rule was confirmed for two of the three species, for the male-biased side of the SSD spectrum, and *A. sphyinx* followed a similar but nonsignificant pattern.

To date, most studies of Rensch's rule in insects, birds, mammals, and reptiles have compared differences among

Fig. 3. Rensch's rule in three Mediterranean blenny species. The broken lines illustrate unity ($y = x$), the solid lines represent the slopes of the relationships between mean male and mean female lengths (L_s): (a) *Microlipophrys canevae*, regression equation: $\text{Log}_{10}(\text{female } L_s) = 0.58 \times \text{Log}_{10}(\text{male } L_s) + 0.64$; (b) *Parablennius incognitus*, regression equation: $\text{Log}_{10}(\text{female } L_s) = 0.41 \times \text{Log}_{10}(\text{male } L_s) + 0.88$; and (c) *Aidablennius sphyinx*, regression equation: $\text{Log}_{10}(\text{female } L_s) = 0.39 \times \text{Log}_{10}(\text{male } L_s) + 0.94$. Scales vary between species.



species (Fairbairn 1997; Colwell 2000; Kratochvil and Frynta 2002; Székely et al. 2004; Johansson et al. 2005; Raihani et al. 2006; Blanckenhorn et al. 2007; Webb and Freckleton 2007). Recent studies, however, indicate that variation in SSD and Rensch's rule also occurs among populations (Young 2005; Blanckenhorn et al. 2006; Fairbairn 2005; Pyron et al. 2007). Young (2005) demonstrated that variation in SSD among geographically separated salmon and trout populations was as large as among species. The findings in our study show a similar pattern: population variation in SSD largely exceeded interspecific variation. Note that in this case, there was a higher probability of genetic exchange among the blenny populations than exists in salmonids, which typically home to natal streams (Quinn 2005). Such high intraspecific variation in SSD, presumably with little underlying genetic variation, will hamper the detection of interspecific patterns.

Most studies share the view that patterns in SSD such as Rensch's rule have a genetic basis, and arise through mechanisms such as a correlated response of males and females to sexual selection (Fairbairn 1997; Székely et al. 2004). However, it is possible that variation among populations in

SSD results from phenotypic plasticity rather than genetic variation (Fairbairn 2005), and therefore reflects varying local conditions. Fierce male–male competition for breeding space and matings occurs in Mediterranean blennies, which can favour large male body size (Almada et al. 1994; Locatello and Neat 2005). Local environmental constraints, such as limited nest site availability, affect mating competition in the blenny system (Almada et al. 1994, 1995). Therefore, it is possible that localized differences in the intensity of intrasexual competition, possibly owing to differences in availability of nest sites, contribute to the interpopulation variation in SSD within our three focal species. Most fish grow indefinitely, which allows greater scope for direct adaptation to changing environmental conditions compared with other taxa such as birds and mammals, which reach maximum size at maturation. The particularly plastic body size of fishes, together with intrasexual competition that is variable in intensity and strongly influenced by environmental conditions (availability of nest sites), may therefore result in greater plasticity of SSD within fish species.

This study does not account for body size differences in animals with indefinite growth that can in part be explained by age differences. Accurately assessing age of the species used for this study would have required an otolith study, and therefore killing all of the fish that were measured. If different mortality rates occur through higher predation on females than males, this could result in the observed male-biased SSD. Local differences in predator abundance could then cause interpopulation variation in SSD. However, in the species used for this study, males are more brightly coloured and ornamented than females and males perform extensive courtship displays. It would therefore be expected that males rather than females would have a higher risk of predation (Wiens 2001), which would make a sexual age difference an unlikely candidate for generating male-biased SSD.

Our study provides an example of a fine-scaled comparative analysis in a previously underrepresented group, and its potential to identify evolutionary patterns that exist within species. This may be a powerful tool to detect patterns and understand their underlying processes. Furthermore, our study demonstrates that variation in SSD among populations can exceed variation among species. Thus, comparisons among populations can provide a useful complement to the more typical use of interspecific comparisons for testing evolutionary theories of SSD.

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