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ORIGINAL PAPER

Disruptive selection by predation offsets stabilizing selection on shell morphology in the land snail *Iberus g. gualtieranus*

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Abstract This work analyses the selection on shell morphology (height and width) in an arid-dwelling land snail with a flattened shell, *Iberus g. gualtieranus*. The findings show absence of selection, but more detailed analyses, separating the effect of different selective agents, show that there is disruptive selection on shell height caused by predation (by black rats, *Rattus rattus*). Nevertheless, this disruptive selection was balanced by stabilizing selection caused by other unknown mortality sources with the same strength. The two selective forces acting in opposite directions resulted in an absence of appreciable selection on shell height. This study suggests that it is important to analyse the effect of different sources of selection acting simultaneously on a trait, in order to attain a precise picture of the selective patterns, especially when the whole selection is close to zero, as this does not necessarily imply the absence of selection on the trait.

Keywords Arid environments · Coefficients of selection · Cubic splines · Natural selection · Phenotypic selection · Predation

Introduction

Natural selection is probably the primary mechanism in evolution (e.g., Fairbairn and Reeve 2001). In order to understand how evolution works, it is important to quantify and classify selection processes in the wild. For this, the coefficients of selection have been developed, these giving standardized estimates of selection, which are useful to compare between different natural systems or populations (Lande and Arnold 1983; Endler 1986; Brodie et al. 1995). This has enabled a major advance in the knowledge of the patterns of

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natural selection (Kingsolver et al. 2001; Hoekstra et al. 2001; Hereford et al. 2004). The coefficients of selection measured in the wild have a median of 0.10−0.16 standard deviations (Kingsolver et al. 2001), although it is probable that these values overestimate the true intensity of phenotypic selection, as there is a publication bias favouring high values of selection (Kingsolver et al. 2001; Hersch and Phillips 2004).

Terrestrial gastropods, usually having a great phenotypic variation in shell traits, constitute a good model for the study of selection processes (Jones 1973). Shell colour and morphology are under predictable natural selection (Cain 1977; Jones et al. 1977; Goodfriend 1986). Many studies have shown selection on shell colouration (e.g., Allen and Weale 2005), or shell morphology (e.g. Reed and Janzen 1999), and, moreover, there is evidence for covariation between shell morphology and environmental conditions that has been related to natural selection on shell morphology (Cameron 1978; Alonso et al. 1985; Emberton 1994; Welter-Schultes 2000; Pfenninger and Magnin 2001).

Iberus gualtieranus gualtieranus is a snail with a flattened shell, which distinguishes it from the subspecies *I. g. alonensis*, which has globular morphology (López-Alcántara et al. 1985; Elejalde et al. 2005). Why flattened shells evolve remains unclear (Teshima et al. 2003). Cain and Cowie (1978) related flat morphology to displacement over horizontal substrates, but this cannot explain the evolution of flat shells in *I. g. gualtieranus*, because this snail is found on substrates with different slopes (Moreno-Rueda 2006). Other authors have related flat morphology to warm climates, where flattened snails can gain access to protective refuges (in crevices or under stones) in order to escape from dryness (de Bartolomé 1982; Goodfriend 1986; Mylonas et al. 1995), given that gastropods are very susceptible to dehydration (Prior 1985; Luchtel and Deyrup-Olsen 2001). The latter hypothesis fits *I. g. gualtieranus* (de Bartolomé 1982; López-Alcántara et al. 1983), since this snail inhabits dry mountains in south-eastern Spain (Alonso et al. 1985), where flattened snails gain more access to sheltering in karstic fissures (unpublished data).

Predation, on the other hand, is one of the primary selective forces on shell colour and morphology in snails (Slotow et al. 1993; Quensen and Woodruff 1997; Schilthuizen et al. 2006). Thus, its influence on the evolution of flattened morphology should also be considered, as flattened snails might use refuges in order to avoid predation.

In the present work, I analyse phenotypic selection by mortality on two traits of shell morphology (height and width) in the snail *Iberus g. gualtieranus*, by comparing morphology between dead and live individuals (Endler 1986). Initially, I failed to detect significant selection, but more detailed analyses revealed that different selective agents acted on shell height in opposing directions, the absence of net selection being a consequence of these opposing forces.

Material and methods

The study was performed in Sierra Elvira (SE Spain, 37° 15′ N, 3° 40′ W) between the years 2002–2004. Throughout the entire population in the sierra (which occupies 300 ha of surface), I randomly collected 184 adult individuals (only adults have a lip in the peristome; Fechter and Falkner 1993). Old shells (recognizable because they are decoloured or full of soil) were discarded. Therefore, patterns of selection described in this paper refer to selection on the whole population. I measured shell height, from the apex to the most convex part in the last whorl, using a calliper (accuracy of 0.01 mm). I also measured the maximal width of the shell (more details of the measurements in López-Alcántara et al.

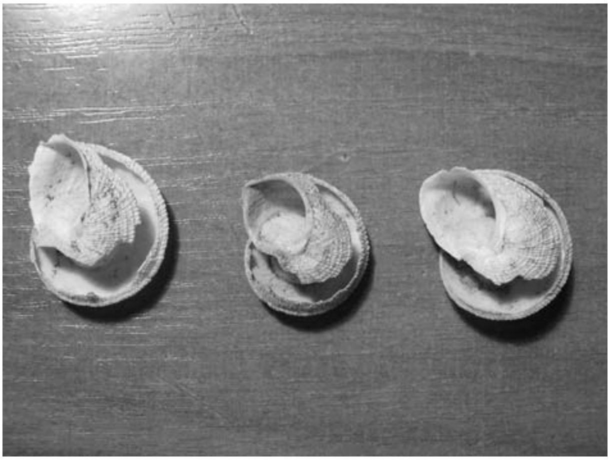

Fig. 1 Photos of some depredated specimens. Note the characteristic marks left by the predator on the shell

1985). Ten shells were measured twice in order to calculate the measurement error (Bailey and Byrnes 1990), which was very low for both characters ($\varepsilon \leq 0.01$).

Although most of the causes of mortality were unknown, individuals that were preyed upon by black rats (*Rattus rattus*) could be distinguished by characteristic marks on the shell (see Fig. 1), as opposed to individuals that died from other causes, with no marks on the shell. The cause of these characteristic marks was identified by a number of criteria. First, broken shells were clumped in small groups homogeneously distributed throughout the population, and rat activity was detected near some groups (primarily, rat's nests). Marks consisted of a crack in the lower part of the shell, without affecting the lip or the protoconche (Fig. 1). Woodruff (1978) described similar marks in *Cerion* as being caused by the Norwegian rat (*Rattus norvegicus*). Other potential predators in the study area were discarded. Birds presents in the study area do not depredate adults of this land snail because of its shell thickness and large size (Yanes et al. 1991), and no arthropods or other mammals that could cause these marks in the shells were detected in the study area. Moreover, some broken shells (not used in the study) were found inside caves, inhabited only by rats and small arthropods. Finally, snail breeders whom I interviewed confirmed that such marks are caused by rats. Natural break up probably was not the cause of this breaking pattern, as it affects the lip of snails in this species (personal observations), which were intact in most of specimens (Fig. 1). Thus, I could differentiate two selective pressures of mortality, one by rat predation, and other by the set of other causes of mortality that showed no traces in the shell (e.g. desiccation, disease, other predators, parasites).

The distribution of residuals approached a normal distribution according to Lilliefor's test, and thus I used the parametric statistic, ANOVA to analyse differences among means, and Levene's test for differences among variances, for the three categories of shells (live, preyed upon, and other causes of mortality) (Sokal and Rohlf 1995).

Estimating the coefficients of selection

The standardized differentials of linear and non-linear selection were computed by using simple linear regressions (Lande and Arnold 1983). In these analyses, morphological variables (height and width, standardized with $\overline{X} = 0$, SD $= 1$) were introduced as independent variables, and the dependent variable was fitness (survival, dead $= 0$, live $= 1/q$; q being the proportion of live individuals (survival rate), modification performed as suggested by Brodie and Janzen (1996)). Differentials of selection correspond to the b coefficient in the linear regression, and they compute the net selection on the target trait, both direct and indirect selection (correlated throughout the selection on other traits). The linear differential of selection (S) indicates whether there is directional selection on the trait. The differential for non-linear selection (c) indicates whether there is quadratic selection on the trait, by an increase of the extreme frequencies in the population (disruptive selection), or by an increase in the intermediate frequencies (stabilizing selection).

I also computed the gradients of selection by using multiple regressions (Lande and Arnold 1983). The gradients of selection measure the direct selection on the trait, controlling for the indirect selection provoked by a correlation of the target trait with the other traits introduced in the model. In this study, only two traits (shell height and width) were used. The linear gradient of selection (β) is analogous to the linear differential of selection (S), and the non-linear gradient of selection (γ) is analogous to the non-linear gradient of selection (c). Selection coefficients are reported with the standard error. Lastly, I also measured the opportunity for selection (I), which is the upper limit for phenotypic selection, using the equation 8C in Brodie and Janzen (1996).

Although selection coefficients are calculated using least-squares, this technique is not appropriate for estimating P-values associated with the coefficients when the distribution of fitness is binomial. For this reason, P-values were estimated using a logistic regression (Mitchell-Olds and Shaw 1987). For a graphic visualization of the selection patterns, I used the cubic-splines (Schluter 1988; Schluter and Nychka 1994), with the program glmsWIN 1.0 (Schluter 2000). Curves were estimated with values of $\lambda = 1$, and 500 bootstraps to estimate the standard error. In cubic-splines, fitness was defined as dead $= 0$, live $= 1$.

In this way, I estimated the "whole selection". In the calculation of selection due to predation, the value of fitness was 0 for depredated individuals, and 1 for live individuals. Similarly, I estimated the selection due to "other causes" assigning a fitness of 0 for individuals that died from "other causes", and 1 for those living.

Results

I collected 70 live and 114 dead individuals, and out of the dead individuals, 54 had been depredated by rats while 60 had died from other causes. Depredated individuals were found homogeneously throughout the population. Average shell width was 28.3 (±SD $= 2.28$) mm, and mean shell height was 12.9 (±SD $= 1.26$) mm. Depredated individuals showed a characteristic pattern of breakage in the lower part of the last spire (Fig. 1). This breakage pattern was associated with predation by black rats (see Section "Material and methods"). The causes of mortality of individuals catalogued as dead from "other causes" were unknown and probably were mixed, but it is improbable that they include the same predators causing the characteristic shell breakage.

Morphological differences

For shell height, there were no significant differences for means among the three categories of individuals (Table 1; $F_{2,\,181} < 0.01$; $P = 1.00$). However, the variance in height significantly differed among categories, being higher for depredated individuals, lower for

Table 1 Values of mean and variance of shell height and shell width, for live individuals, depredated specimens and individuals that died from "other causes"

	Height		Width	
	Mean (mm)	Variance	Mean (mm)	Variance
Live	12.9	1.42	28.2	4.41
Depredated	12.9	0.71	28.4	4.2
Other causes	12.9	2.59	28.2	7.13

Table 2 Standardized coefficients of selection ± standard error for events of selection by predation, by "other causes" of mortality, and the whole selection

	$S \pm$ SE	$c \pm$ SE	$\beta \pm$ SE	$\gamma \pm$ SE
Height				
Selection by predation	−0.034 ± 0.092	0.186 ± 0.092*	0.058 ± 0.122	0.275 ± 0.111**
Selection by other causes	0.098 ± 0.103	−0.188 ± 0.103*	0.121 ± 0.156	−0.117 ± 0.133
Whole selection	0.026 ± 0.084	−0.050 ± 0.084	0.087 ± 0.121	−0.007 ± 0.101
Width				
Selection by predation	−0.058 ± 0.091	0.008 ± 0.091	−0.152 ± 0.123	−0.159 ± 0.111
Selection by other causes	0.038 ± 0.091	−0.168 ± 0.091*	−0.033 ± 0.141	−0.109 ± 0.119
Whole selection	−0.019 ± 0.075	−0.075 ± 0.075	−0.080 ± 0.112	−0.084 ± 0.092

S, linear differential of selection; *c*, non-linear differential of selection; β, linear gradient of selection; γ, non-linear gradient of selection. Values of *P* were calculated with a logistic regression: * $P \leq 0.10$, ** $P < 0.05$

specimens that died from other causes, and intermediate for live snails (Table 1; Levene's test, $F_{2,\ 181} = 6.10$; $P < 0.001$). Pairwise tests showed significant differences in variance between depredated individuals and those that died from other causes (Levene's tests; $F_{1,\ 112} = 11.26$; $P = 0.001$), and almost significant differences among live individuals and the other two groups ($F_{1,\ 122} = 3.54$; $F_{1,\ 128} = 3.57$; $P = 0.06$ in both cases). This finding suggests that there was disruptive selection on shell height by predation, while other causes of mortality provided stabilizing selection on shell height. For shell width, there were no differences for mean or variance between live and dead individuals ($F_{2,\ 181} = 0.19$; $P = 0.83$; Levene's test, $F_{2,\ 181} = 2.10$; $P = 0.13$; Table 1).

Coefficients of selection

Table 2 shows the standardized coefficients of linear and non-linear selection for each selection event: selection by predation, selection by "other causes", and whole selection. Differentials of selection showed the net selection on traits in each event. For shell height, mortality for other causes provoked an almost significant non-linear selection on shell height of $c = -0.188$ (i.e., stabilizing; Fig. 2a). The non-linear selection by predation on shell height, in turn, went in the opposite direction, suggesting a disruptive selection with similar strength ($c = 0.186$; Fig. 2b). As a result, selection provoked by predation seemed to offset selection by "other causes", leading to a differential of non-linear selection for whole selection of only $c = -0.05$ (Fig. 2c; Table 2).

Shell height and shell width were correlated ($r = 0.74$; $P < 0.001$; $n = 184$), and thus, in order to control for indirect selection, I calculated the gradients of selection (Table 2). No gradient of linear selection significantly differed from zero (Table 2). Direct selection by predation on shell height was significant and disruptive ($\gamma = 0.275$), and it was higher

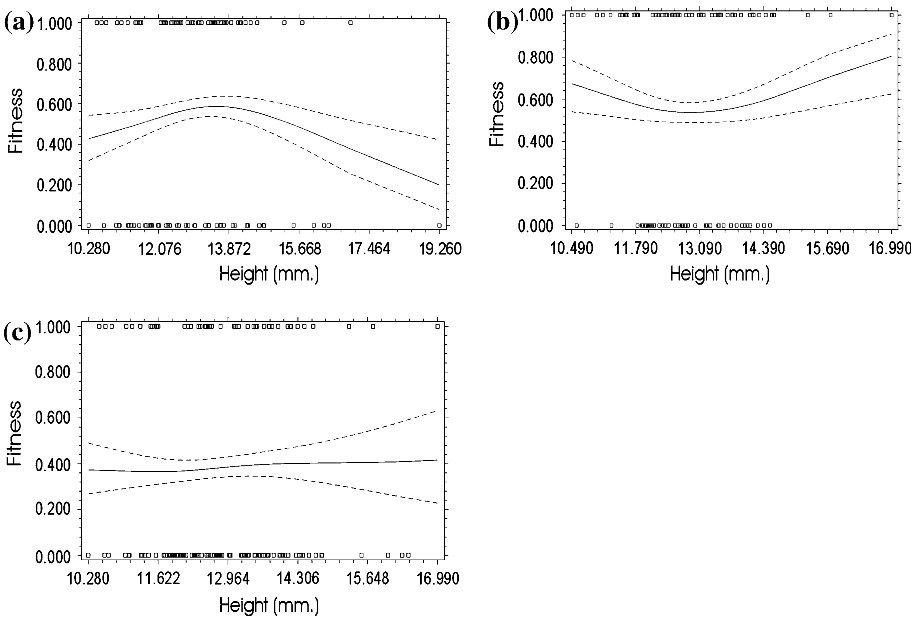

Fig. 2 Non-parametric estimates of selection on shell height, using cubic-splines (continuous line). The broken line shows the standard error. (**a**) selection by "other causes" of mortality, (**b**) selection by predation, (**c**) whole selection

than the net selection measured by the differentials (previous paragraph), suggesting that correlated selection on width diminished the whole effect of predation on height (see selection on shell width in Table 2). Direct selection by "other causes", in turn, was lower, and stabilizing (Table 2), suggesting that the net selection by "other causes" was increased by correlated selection on width. The whole direct selection had a gradient of non-linear selection close to zero ($\gamma = -0.007$).

Lastly, the opportunity for selection due to predation was $I = 0.771$, while the opportunity for selection due to "other causes" of mortality was similar, $I = 0.857$. The opportunity for selection in total was $I = 1.632$. Figure 2 shows a possible outlier for shell height (19.26 mm). I repeated all the analyses without this datum, but all the findings were similar (data not shown), and thus this point seemed not to affect the results.

Discussion

The present study shows the selection patterns on the whole population of *Iberus g. gualtieranus*. It has not been disregarded that selection patterns can vary geographically inside the population (the present study covers an area of 300 ha). However, when the whole population is considered, a complex picture emerges with regard to the selection patterns in this species. The findings suggest disruptive selection on shell height in this snail, caused by rat predation. Depredation on intermediate phenotypes may be one the most frequent causes for disruptive selection (Rueffler et al. 2006). Reed and Janzen (1999), for example, also reported disruptive selection by predation on the shell size in the snail *Pomacea flagellata*. In the species studied here, snails with more depressed shells can use fissures as refuges more easily than can individuals with high shells (unpublished data), and thus, snails with the narrowest shells could enter refuges that are more inaccessible for predators. This would reduce predation on snails with low shells. Difficulties in handling large prey might explain why predators barely prey on snails with high shells. This, moreover, could provoke a learned preference for average phenotypes by rats.

However, when other mortality causes besides predators were considered, selection on shell height was stabilizing (although not significantly). That is, these causes of mortality preferentially affected the highest and the lowest shells. Part of this selection was indirect (i.e., correlated) through a weak selection on shell width. This pattern of selection balanced the selection caused by predation, and thus, the whole selection on shell height, considering all sources of mortality and indirect selection via selection on width, was very low and did not significantly differ from zero (Table 2; Fig. 2c). The causes of this unknown source of mortality were probably mixed. More globose snails have difficulties in to use fissures, the most protective refuges against dehydration, as shelter, and it is possible that these specimens had a higher risk of dying from desiccation. On the other hand, more flattened snails have a lower body volume, and thus less capacity to store reserves and to survive the periods of aestivation (Arad et al. 1995), which can last six months in the study area (unpublished data).

Kingsolver et al. (2001) found a median value of 0.10 for gradients of non-linear selection, although these values seem to overestimate the true strength of selection (Hersch and Phillips 2004). In this study, gradients of non-linear selection due to predation doubled those reported. In turn, when the whole selection was measured, the gradient of non-linear selection was only $\gamma = -0.007$, and it could be concluded that there was no selection on shell morphology in this snail. In the analysis of the effect of predation and “other causes” of mortality, the complete picture showed that there were really two opposing selections on shell height. For a comprehensive study of the mechanisms of natural selection, it is necessary to ascertain the strength with which the selection is acting, and on which traits, and this includes determining the traits for which and under what conditions the strength of the selection is close to zero. There are different reasons why selection may be zero, and each factor has different implications on evolution:

(1) Selection would be near to zero or null if the opportunity for selection is very low or null (Arnold and Wade 1984). In this study, the opportunity for selection was not low ($I = 1.632$). (2) Selection would be null or very low if the variance in fitness does not covary or covaries only slightly with the phenotype (Fairbairn and Reeve 2001). In this case, it should be asked why covariation between fitness and phenotype is near to zero. (2a) A possibility is that the variance of phenotype has no effect on fitness; then, selection is not acting and phenotypic variation is due to other processes (e.g., plasticity; Mazer and Damuth 2001). (2b) Another possibility is that different selective pressures (direct or indirect selections) act on the target trait in opposite directions, in the same or different selection episodes, so that the sum of the selection vectors gives a selection coefficient of close to zero. The latter explains the absence of selection on shell height in the present study, and similar patterns have been found in other studies (e.g. Gómez 2003). In this case, although different selective forces act on the target trait, the response to selection would be low. However, if differences in mortality translate into differences in fitness, changes in the environment (for example, the extinction of the predator), would provoke changes in the relative effect of the selective agents, and evolution would occur. For this reason, it is important to distinguish between the situation 2b and the both situations 1 and 2a.

In conclusion, no selection by mortality on shell morphology was found in the snail *Iberus g. gualtieranus* in this study. However, when the effects of two selective agents were considered separately, it was found that predation by rats provoked a disruptive selection on shell height, which seemed to be balanced by a stabilizing selection by other causes of mortality. Therefore, researchers should be cautious when no selection is detected, and should try measuring the effect of different selective pressures that may be acting in opposite directions.

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