BIOCHEMISTRY

Correction for "The *Corynebacterium diphtheriae* shaft pilin SpaA is built of tandem Ig-like modules with stabilizing isopeptide and disulfide bonds," by Hae Joo Kang, Neil G. Paterson, Andrew H. Gaspar, Hung Ton-That, and Edward N. Baker, which appeared in issue 40, October 6, 2009, of *Proc Natl Acad Sci USA* (106:16967–16971; first published September 21, 2009; 10.1073/pnas.0906826106).

The authors note that, due to a printer's error, on page 16967, the keyword "**mas spectromrtry**" should instead have appeared as "**mass spectrometry**." The online version has been corrected.

www.pnas.org/cgi/doi/10.1073/pnas.0911293106

CELL BIOLOGY

Correction for "CBP and p300 are cytoplasmic E4 polyubiquitin ligases for p53," by Dingding Shi, Marius S. Pop, Roman Kulikov, Ian M. Love, Andrew Kung, and Steven R. Grossman, which appeared in issue 38, September 22, 2009, of *Proc Natl Acad Sci USA* (106:16275–16280; first published September 4, 2009; 10.1073/pnas.0904305106).

The authors note that the author name Andrew Kung should instead have appeared as Andrew L. Kung. The online version has been corrected. The corrected author line and author contributions footnote appear below.

Dingding Shi, Marius S. Pop, Roman Kulikov, Ian M. Love, Andrew L. Kung, and Steven R. Grossman

Author contributions: D.S., M.S.P., R.K., and S.R.G. designed research; D.S., M.S.P., R.K., and I.M.L. performed research; A.L.K. contributed new reagents/analytic tools; D.S., M.S.P., R.K., and S.R.G. analyzed data; and S.R.G. wrote the paper.

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ECOLOGY

Correction for "Adaptive shell color plasticity during the early ontogeny of an intertidal keystone snail," by Patricio H. Manríquez, Nelson A. Lagos, María Elisa Jara, and Juan Carlos Castilla, which appeared in issue 38, September 22, 2009, of *Proc Natl Acad Sci USA* (106:16298–16303; first published September 2, 2009; 10.1073/pnas.0908655106).

The authors note that on page 16298, right column, first full paragraph, the first sentence appeared incorrectly in part. "In the rocky intertidal habitats dominated by mussel beds (dark colored) and barnacle stands (light colored), we found that more than 95% of early postmetamorphic stages of *C. concholepas* (≈2 to 20 mm **periostomal** length, PL) showed a striking color-matching with the most abundant prey (Fig. 2 *A* and *B*)" should instead have appeared as "In the rocky intertidal habitats dominated by mussel beds (dark colored) and barnacle stands (light colored), we found that more than 95% of early postmetamorphic stages of *C. concholepas* (≈2 to 20 mm **peristomal** length, PL) showed a striking color-matching with the most abundant prey (Fig. 2 *A* and *B*)." Additionally, the authors note that on page 16301, right column, first full paragraph, the second sentence did not appear in full due to a printer's error. The sentence should instead have appeared as "This modulation of the shell coloration is restricted to snails of small size (ca. less than 3 cm), coincidentally the size at which *C. concholepas* appear to escape predation by crabs (author's personal observations)." These errors do not affect the conclusions of the article.

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Adaptive shell color plasticity during the early ontogeny of an intertidal keystone snail

Patricio H. Manríquez[a,1], Nelson A. Lagos[b], María Elisa Jara[a], and Juan Carlos Castilla[c,1]

[a]Instituto de Biología Marina ''Dr. Jürgen Winter,'' Laboratorio Costero de Recursos Acuáticos de Calfuco, Facultad de Ciencias, Universidad Austral de Chile, Casilla 567, Valdivia, Chile; [b]Centro de Investigación en Ciencias Ambientales, Departamento de Ciencias Básicas, Universidad Santo Tomás, Ejercito 146, Santiago, Chile; and [c]Departamento de Ecología and Center for Advanced Studies in Ecology and Biodiversity, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

Contributed by Juan Carlos Castilla, August 5, 2009 (sent for review March 31, 2008)

We report a mechanism of crypsis present during the vulnerable early post-metamorphic ontogeny (≤20 mm peristomal length) of the muricid snail *Concholepas concholepas,* a rocky shore keystone predator characteristic of the southeastern Pacific coast. In the field, we found a significant occurrence (>95%) of specimens bearing patterns of shell coloration (dark or light colored) that matched the background coloration provided by patches of *Concholepas'* most abundant prey (mussels or barnacles respectively). The variation in shell color was positively associated with the color of the most common prey ($r = 0.99$). In laboratory experiments, shell coloration of *C. concholepas* depended on the prey-substrate used to induce metamorphosis and for the post-metamorphic rearing. The snail shell color matched the color of the prey offered during rearing. Laboratory manipulation experiments, switching the prey during rearing, showed a corresponding change in snail shell color along the outermost shell edge. As individuals grew and became increasingly indistinguishable from the surrounding background, cryptic individuals had higher survival (71%) than the non cryptic ones (4%) when they were reared in the presence of the predatory crab *Acanthocyclus hassleri*. These results suggest that the evolution of shell color plasticity during the early ontogeny of *C. concholepas,* depends on the color of the more abundant of the consumed prey available in the natural habitat where settlement has taken place; this in turn has important consequences for their fitness and survivorship in the presence of visual predators.

cripticity | mollusk | survivorship

Color changes are examples of phenotypic plasticity, the ability of a single genotype to modify its phenotype under heterogeneous environmental conditions (1). The evidence of phenotypic and developmental plasticity recorded in animal and plant taxa is significant, and the maintenance of this plasticity within populations is a key subject in ecological and evolutionary studies (2, 3). Although most studies on the relationship between plasticity and adaptation have ignored the consequences on fitness (4), environmentally determined body coloration and its consequences for predator avoidance is a good example for testing whether phenotypic plasticity is adaptive (5). Because the environment is often a mosaic of patches with contrasting distribution of color background patterns (6), phenotypic plasticity may represent a generalist strategy evolved by cryptic species to avoid visual predation. Consequently, in species with cryptic coloration, survivorship in the presence of visual predators should improve as they blend with the surrounding background (7–10).

On exposed rocky intertidal shores of the southeastern Pacific, the carnivorous gastropod *Concholepas concholepas,* a keystone predator, drives the intertidal distribution and abundance of the dominant space occupier, the mussel *Perumytilus purpuratus,* and subordinate species such as barnacles which form part of its prey assemblage (11). During its early post-metamorphic and early juvenile stages, *C. concholepas* is vulnerable to visual predation by organisms such as intertidal crabs, birds and rats (12–16). The environment in which the early ontogeny of this species takes place is conformed by a mosaic of prey patches with contrasting color (i.e., mussels and barnacles among other species). This suggests that during the early ontogeny of species with complex life cycle, as with *C. concholepas* and other benthic marine invertebrates, natural selection may favor the evolution of color plasticity as a mechanism of crypsis. Using field and laboratory evidence we demonstrate that the shell coloration pattern of *C. concholepas* during early ontogeny depends on the color of consumed prey that are more abundant in the settlement habitat (Fig. 1), and this in turn affects their survival and therefore may have important consequences on fitness.

Results and Discussion

Shell Coloration in the Field. In the rocky intertidal habitats dominated by mussel beds (dark colored) and barnacle stands (light colored), we found that more than 95% of early postmetamorphic stages of *C. concholepas* (≈2 to 20 mm periostomal length, PL) showed a striking color-matching with the most abundant prey (Fig. 2 *A* and *B*). Additionally, we found that approximately 70% of those ontogenetic stages, occurring in habitats co-dominated by mussel and barnacle, showed mixed shell coloration patterns matching the dominant background color (binomial probability, $P < 0.0001$, Fig. 2*A*). We found that red-green-blue (RGB, see *Materials and Methods*) values recorded from shells of early post- metamorphic *C. concholepas* showed a positive and significant association with the RGB values recorded for their native substrate (Fig. 2*B*).

Shell Coloration and Consumed Prey Items. In the laboratory experiments with competent larvae, about 2 h after metamorphosis, the gold-colored protoconch of *C. concholepas* became dark regardless of the prey provided (Fig. 1 *A–D*), but 2 days later newly added shell material of *C. concholepas* showed a coloration and RGB values similar to the prey color (Figs. 1 *A–D* and 3*A*). Significant variation in shell color between laboratory reared individuals on different diets was found [ANOVA between subject comparison for diet, $F_{(2, 33)} = 497$, $P = 0.0001$]. These differences in shell color persisted over time (ANOVA within subject comparison for diet × time, $F_{(8, 132)} = 154$, $P = 0.149$]. Within each experimental diet, similar RGB values were observed between the newly generated shell after 8 and 28 days of rearing [ANOVA repeated measures, a priori contrast, $F_{(2, 33)} = 1.17$, $P = 0.322$].

A predictable shift in shell RGB values of *C. concholepas* took place after the experimental prey-switch (Fig. 3*B*). Dark individuals which had been reared on mussels diet developed a contrasting light shell border 14 days after a prey-switch to

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The authors declare no conflict of interest.

[1]To whom correspondence may be addressed. E-mail: pmanriquez@uach.cl or jcastilla@bio.puc.cl.

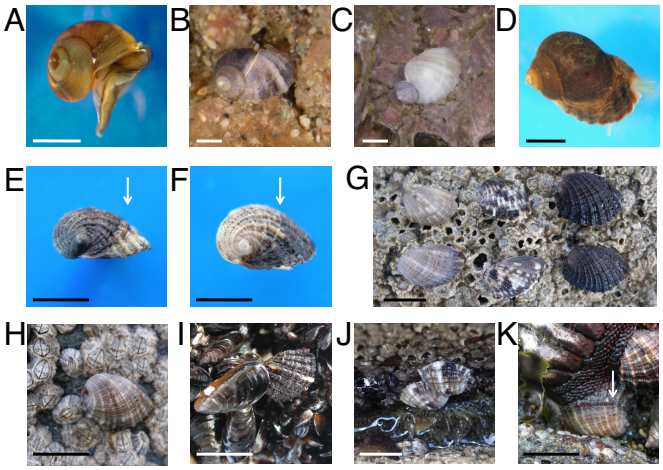

Fig. 1. Shell of the gastropod *Concholepas concholepas*. (*A*) Goldish protoconch of competent larvae collected from the plankton. (*B*) Mixed color teleoconch of a post-metamorphic juvenile fed on a mix of *N. scabrosus* and *P. purpuratus*. (*C*) Light colored teleoconch of a post-metamorphic juvenile fed on *Notochthamalus scabrosus*. (*D*) Dark colored teleoconch of a post-metamorphic juvenile fed on *Perumytilus purpuratus*. (*E*) A prey-switched specimen fed on *P. purpuratus* and then on *N. scabrosus*. (*F*) A prey-switched specimen fed on *N. scabrosus* and then on *P. purpuratus*. (*G*) Specimens cultured in the laboratory with light, mixed and dark colored diets placed against a small rock covered with barnacles. (*H*) A light colored specimen on a barnacle stand of *N. scabrosus*. (*I*) A dark colored specimen on a mussel bed of *Semimytilus algosus* (*J*) Two specimens from a mixed wild prey-substrate. (*K*) A prey switched shell color specimen from the field. Because the photographed specimens were chosen to illustrate the shell color pattern they may not correspond with the snail sizes described in the experiments. In *E*, *F*, and *K*, the arrows indicate the change in shell color. [Scale bars, 1 mm (*A–D*) and 10 mm (*E–K*).]

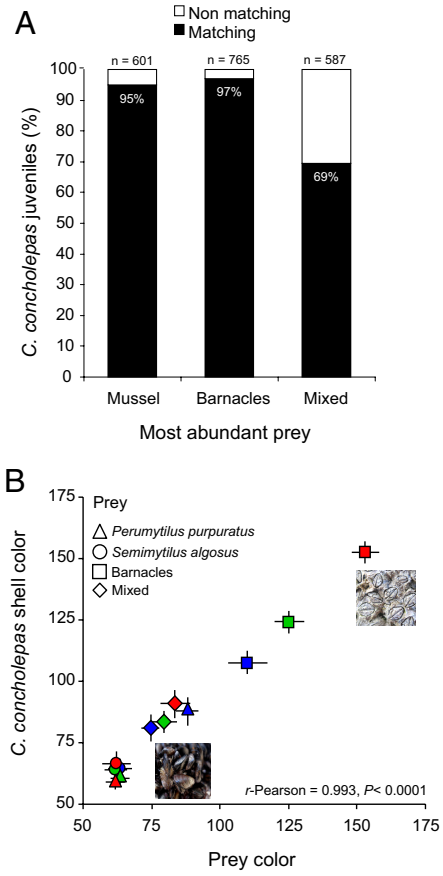

Fig. 2. (*A*) Relative abundance of *Concholepas concholepas* with shell color matching and non-matching the surrounding color recorded in three intertidal microhabitats. The microhabitats were characterized according the most abundant prey item: dark habitats dominated by the mussels *Perumytilus purpuratus* and *Semimytilus algosus*, light colored habitat dominated by barnacles of *Jehlius cirratus*, *Notochthamalus scabrosus*, *Notobalanus flosculus*, *Balanus laevis*, and mixed habitat with both prey taxa. The snails were photographed and then categorized as light, dark and mixed colored. Matching and non-matching snails were considered as those that did or did not have the same color category as the prey on which they were found. Color categorization and the determination of whether they matched the prey color or not were determined by visual inspection. (*B*) Relationships between the mean RGB values (±1 SE) of background and shell of *C. concholepas* ($n = 10$). Symbols are filled with the corresponding r(ed), g(reen) and b(lue) analyzed color.

barnacles [ANOVA within subject comparison for prey × time, control = no prey switch, $F_{(4, 88)} = 501$, $P = 0.0001$]. The change in shell RGB value was evident when comparing values recorded after 8 and 28 days of rearing [ANOVA repeated measures, a priori contrast, $F_{(1, 22)} = 587$, $P = 0.0001$]. In agreement with these results, light colored individuals developed a dark shell border just 8 days after the prey-switch to mussels [ANOVA within subject comparison for diet × time, control = no prey switch individuals, $F_{(4, 88)} = 233$, $P = 0.0001$]. As above, this color change was evident when comparing between the RGB values recorded after 8 and 28 of rearing [ANOVA repeated measures, a priori contrast, $F_{(1, 22)} = 192$, $P = 0.0001$]. No changes in coloration were evident in shell areas generated before the prey-switch took place. Shells with banding, dark followed by light colored bands or vice versa, were obtained by switching the diet during the experimental period (Figs. 1 *E* and *F*, and 3 *B* and *D*). These results indicate the role played by the diet at settlement and during the early benthic ontogeny upon modulation of shell color in *C. concholepas*. Similar to the experiments on competent larvae, dark and light colored shells for recently settled individuals were obtained by feeding them with diets of mussels or barnacles, respectively.

The shell color of recently metamorphosed *C. concholepas* collected from intertidal habitats in Antofagasta (northern Chile) all had similar RGB values indicating that, at the start of the experiment, all settlers expressed a common shell coloration pattern [ANOVA, $F_{(3, 62)} = 1.34$, $P = 0.2681$, Fig. 3*C*]. However, these similarities in shell color did not persist over time when juveniles were reared on single prey item diets (mussels or barnacles) [ANOVA between subject comparison for diet × time, $F_{(7, 217)} = 47.89$, $P = 0.149$; Fig. 3*C*]. At the end of the first growth phase, individuals from within each treatment did not exhibit dissimilarities in shell coloration patterns [barnacles: $F_{(1, 31)} = 0.65$, $P = 0.4257$; mussels: $F_{(1, 31)} = 1.14$, $P = 0.2934$; Figs. 3*C* and 4 *A* and *C*]. During the second growth phase, a predictable change in shell color of *C. concholepas* occurs after the experimental shift in diet (Figs. 3*D* and 4). The darker individuals reared on mussels developed a lighter shell borders after a prey-switch to barnacles [ANOVA within subject comparison for prey × time, control = no prey switch, $F_{(7, 217)} = 50.57$, $P < 0.0001$; Fig. 4*B*]. The change in shell color was evident when comparing RGB values recorded on the shell border after 28 and 56 days of rearing [ANOVA repeated measures, a priori contrast, $F_{(1, 31)} = 97.96$, $P < 0.0001$]. In addition, lighter individuals developed a contrasting darker shell border after the prey-switch to mussels [ANOVA within subject comparison for diet × time, control = no prey switch individuals, $F_{(7, 217)} = 233$, $P = 0.0001$; Fig. 4*D*], and this change in shell color was also evident when comparing RGB values of the shell border recorded after 28 and 56 days of rearing [ANOVA repeated measures, a priori contrast, $F_{(1, 31)} = 101.1$, $P < 0.0001$].

Experimental snails used in all treatments had a similar size at the beginning of the experiment. However, we found that growth

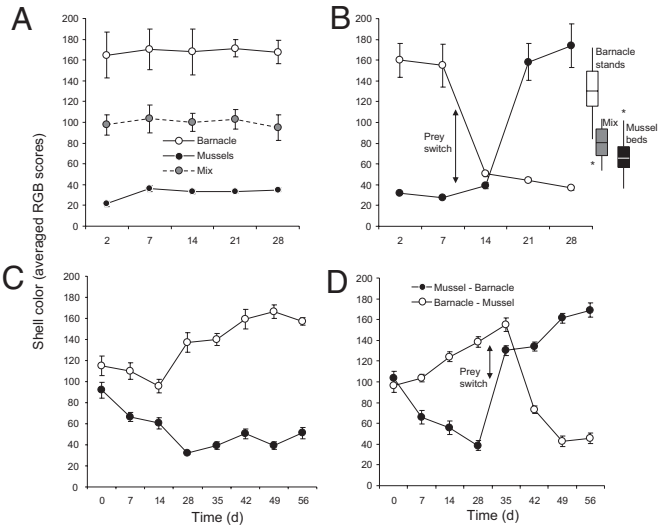

Fig. 3. Changes in shell color of early settlers (mean pooled RGB scores, ± 1 SD, $n = 12$) and post-metamorphic of *Concholepas concholepas* (mean pooled RGB scores, ± 1 SD, $n = 6$). Early settlers were reared over time from 2 days after metamorphosis to 28 days on different colored diets. Three sets of snails were reared during the experiment with light (barnacles stands), dark (mussels beds) and mixed (both taxa) colored prey (*A*). Two sets of snails were reared during the first week with one type of prey and then switched (arrow) to the alternative color prey. The right box plot shows the distributional characteristics of averaged RGB values recorded in natural habitats dominated by the experimental prey (*B*). Postmetamorphic larvae were reared from settlers to 56 days old with different colored diets. Two sets of snails ($n = 6$) were reared during the entire period with light (barnacles) and dark (mussels) prey (*C*). Two sets of snails ($n = 6$) were reared for the first 28 days with one type of prey and then switched (arrow) to the alternative prey (*D*).

rates were significantly higher under a mussel and mussel-barnacle mix diets than under a barnacle diet (Table 1). Fast growing specimens are much darker than slow growing (light colored) ones. Early studies on herbivorous mollusks suggest that shell pigmentation is mainly the result of acid soluble pigments secreted as part of the normal metabolic disposal processes (17). However, more recent studies on carnivorous taxa (18) suggest that this may not be the case and that polyene pigments may have a structural function in the formation of layers of the outer shell matrix. Therefore the physiology of different pigments may depend on the diet, which in the case of *C. concholepas* comprise mainly animal material.

Shell Coloration and Survival. Both light and dark colored snails were lethally attacked and consumed by the intertidal predatory crab *A. hassleri* (cryptic individuals = 29%; non-cryptic = 96%; $n = 24$. Fig. 5), and their survival showed a significant dependence on the level of color matching with the nearby background (cryptic = 71%, non-cryptic = 4.0%, $n = 24$). The estimated change in the log of P (survival)/P (lethal attack) for non-cryptic snails was negative (binary logistic regression, parameter = −4.071 ± 1.14 SD; Wald-$\chi^2 = 12.70$, $P > \chi^2 = 0.0004$) and odds ratio was 0.02 (0–0.16, 95% confidence interval). This indicates that at the end of the experiment, the chances of survival of non-cryptic snails represent only 2% of cryptic ones. This suggests that among habitats differences in frequency of shell color (Fig. 1 *B–K*) may be the result of differential vulnerability of cryptic and non-cryptic snails to a visual predator, such as *A. hassleri* (for crabs as visual predators see 19–21).

In the field, the high occurrence of early postmetamorphic of *C. concholepas* with a shell color matching the native background color suggests that during their early ontogeny (≤20 mm) shell color is modulated by the presence and/or consumption of the

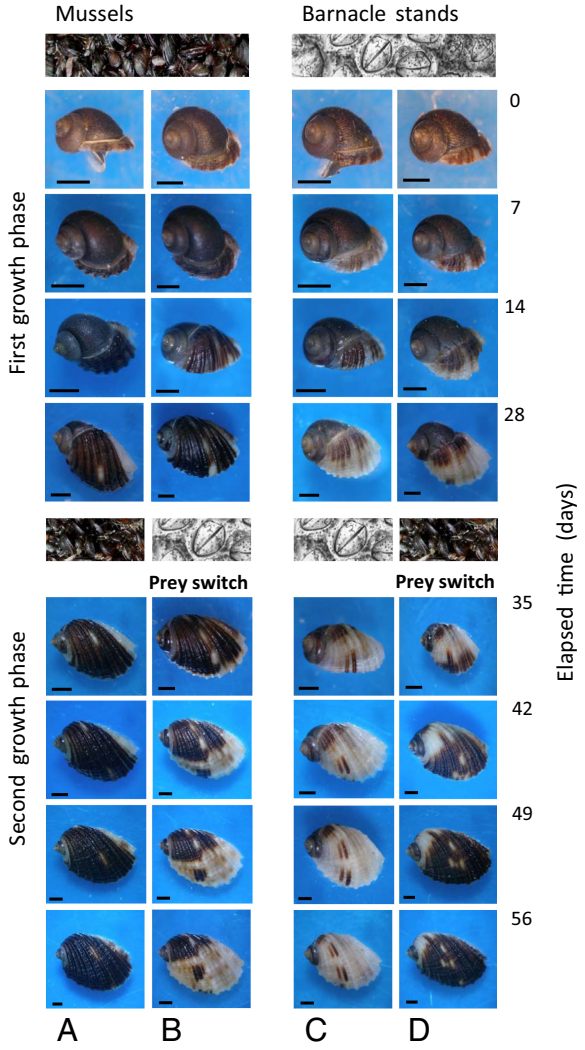

Fig. 4. Photographic summary of a laboratory experiment to test for shell color plasticity in early post-metamorphic *Concholepas concholepas* collected from rocky intertidal habitats in Antofagasta. Each photographic series (*A–D*) represent the two consecutive growth phases of four food treatments. In two treatments the consecutive phases (1–56 days) were conducted with a single prey item; mussels (*Semimytilus algosus*) (*A*) and barnacles (*Jehlius cirratus* and *Notochthamalus scabrosus*) (*C*). In the other two treatments, after the initial growth phase (1–28 days) with a one prey item the diet was switched to the contrasting colored prey (*B* and *D*) for the final phase (29–56 days). In each photographic sequence (*A–D*), the photographs depict growth (scale bar, 1 mm) and shell color of the same individual snail over the entire experimental period.

dominant prey present in the intertidal habitats. This may be a strategy evolved to gain advantage and improve survival in presence of visual predators such as birds and crabs to which small *C. concholepas* are exposed in these habitats (12, 15). The existence of background color matching or crypsis in this species agrees with predictions regarding the important role of animal color patterns and camouflage (7–10). Given the matching of *C. concholepas* color with nearby surroundings under field conditions, and the improved survivorship of matching snails under laboratory conditions, we suggest that phenotypic plasticity in *C. concholepas* may assist this species in evading predation by *A. hassleri,* which may use visual cues to detect their prey. This behavior is supported by spectral sensitivity and retinal pigments studies conducted in crabs, suggesting that visual stimuli affect

Table 1. Body size and growth rate (average ± 1 SD) of post-metamorphic individuals and recently settled specimens of *C. concholepas* under different diet treatments conducted in laboratory conditions for 28 and 56 days respectively

Diet treatments	*N*	Initial size, mm	Final size, mm	Growth rate, mm·d^{-1}
Postmetamorphic specimens				
Barnacles	12	1.89 ± 0.04^a	12.34 ± 0.78^a	0.37 ± 0.03^a
Mussels	12	1.84 ± 0.06^a	16.39 ± 1.24^b	0.52 ± 0.04^b
Mixed	6	1.89 ± 0.05^a	17.41 ± 1.24^b	0.55 ± 0.02^b
Recently settled specimens				
Barnacles	6	1.48 ± 0.04^a	3.64 ± 1.25^a	0.03 ± 0.02^a
Mussels	6	1.55 ± 0.10^a	6.15 ± 0.66^b	0.08 ± 0.01^b
Barnacles to Mussels	6	1.48 ± 0.04^a	5.50 ± 0.31^b	0.55 ± 0.02^b
Mussels to Barnacles	6	1.53 ± 0.05^a	5.72 ± 0.50^b	0.08 ± 0.01^b

The superscripts for the postmetamorphic specimens indicate significant differences ($P < 0.05$, Tukey test as *post-hoc* comparison) in size at the beginning (ANOVA, $F_{2,27} = 2.22$, $P = 0.128$), at the end (ANOVA, $F_{2,27} = 73.68$, $P < 0.0001$) of the rearing experiment, and in daily growth rates (ANOVA, $F_{2,27} = 72.30$, $P < 0.0001$). The superscripts for recently settled specimens indicate significant differences in size at the beginning (ANOVA, $F_{3,23} = 1.67$, $P = 0.206$), at the end (Log data, ANOVA, $F_{3,21} = 11.66$, $P < 0.0001$) of the rearing experiment, and in daily growth rates estimates (ANOVA, $F_{3,23} = 14.49$, $P < 0.0001$). Postmetamorphic specimens were obtained by metamorphosing in the laboratory competent larvae collected in the field and then reared in the laboratory under the experimental diet treatments. Recently settled specimens were collected in the field and then reared in the laboratory under the experimental diet treatments.

their predatory strategy and that they can respond to visual stimuli received from prey (20, 21).

Shell color variation among marine snails may be governed by environmental (22–24) or by genetic factors (25–27). Gene flow in *C. concholepas* appears to be high because potential for larval dispersal is so much larger in scale for the species (≈3 months of pelagic life, 28) than the distance between patches of their prey (i.e., barnacles or mussels). Therefore, local adaptation to one or other prey it is not possible and natural selection must favor adaptive and flexible responses such as the evolution of color plasticity. Our laboratory results showed that shifting between prey with contrasting colors was followed by a shift in the coloration of the newly generated shell of *C. concholepas*, which matched the color of the new prey. This indicates that color plasticity may be determined by the available diet at settlement and early life stages. This agrees, for instance, with the suggestion of ecological control of color polymorphism in the seastar *Pisaster ochraceus*, where the expression of orange-brown pigmentation is correlated with consumption of *M. californianus,* while brilliant purple is more common among seastars lacking access to this prey (29). In benthic species with complex-life cycles, larval dispersal must confront the arrival and settlement into uncertain environments. Thus, diet-controlled color plasticity may represent a mechanism providing a significant fitness advantage in post-metamorphic settlers and juveniles faced with a new and variable environment (e.g., 30).

Our results indicate that the presence of prey items modulate and maintain the shell color variation within early ontogenetic stages of *C. concholepas* and that between-habitat variation in this snail's shell color frequency may reduce vulnerability to visual predators like crabs. This modulation of the shell coloration is restricted to snails of small size (*C. concholepas* appear to escape predation by crabs (author's personal observations). Therefore, our results show the value of incorporating early ontogenetic traits, such as shell color plasticity which may have important consequences for the fitness of organisms with complex life-cycles, into studies of trophic interactions (31). Finally, the capacity of *C. concholepas* to change its shell color to match that of its prey species represent a mechanism that, so far, has not been convincingly demonstrated for any caenogastropod (32).

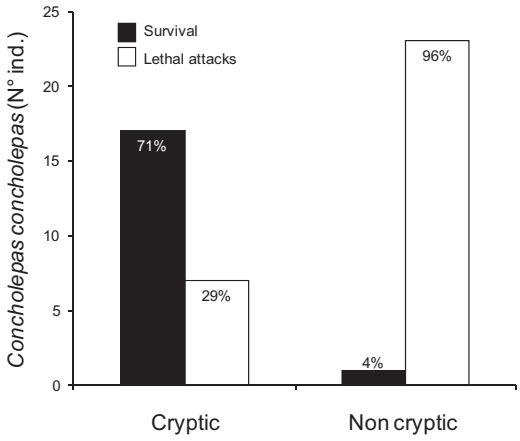

Fig. 5. *Concholepas concholepas* survival and lethal attacks by the crab *Acanthocyclus hassleri* in shell matching and non-matching color background. Dark snails are cryptic on mussel backgrounds, while non cryptic on barnacles stands.

Materials and Methods

Shell Coloration in the Field. We conducted field surveys to characterize the shell coloration of early settlers and small juvenile snails of *C concholepas* (≈2 and 10 mm in length, respectively) present in different colored intertidal microhabitats at Las Cruces (32°43′ S: 71°38′ W, in 2002–2005) and Calfuco (39°46′ S: 73°23′ W, in 2007). We searched for *C. concholepas* on intertidal platforms dominated by the mussels *P. purpuratus* and *Semimytilus algosus* (the dark colored microhabitat), and intertidal pools with rock boulders incrusted with barnacles such as *Notobalanus flosculus,* unidentified serpulid polychaete and several encrusting colonies of bryozoans (the light colored microhabitat). We also searched for snails on intertidal rocky platforms characterized by the co-dominance of white and dark colored prey described above (the mixed microhabitat). All sampled snails were photographed in situ and according to their shell coloration and were assigned subjectively by eye to the categories: light, dark and mixed. Shells with light and dark colored areas were considered as mixed, and those with an approximately pure color, as light or dark snails. Once the snails were categorized, matching or non matching snails were defined as those that did or did not have a shell color category similar to the microhabitat in which they were recorded; this was assessed by reference to the corresponding photograph. To minimize the potential bias in assessing the shell color, the scoring was repeated three times by different observers. To ensure our observations were objective, from each of the three sampled microhabitats, 10 photographs of small snails (≈2–10 mm) were randomly chosen and RGB analyses conducted (33, 34), in which a color value of 0 corresponds to black and a color value of 255 to white. Each photograph was included the shell as well as the nearby surrounding substrate area and each object processed independently. The analyses used three transects of 250 pixels each randomly placed over photograph areas cropped from the shell surface (parallel to, and within approximately 5 mm of the growth margin of the shells) and over the nearby surrounding substrate (located no more than two body lengths away from the target specimen and placed parallel to the growth margin of the shells). Transects were made using Image-Pro 6.2 analyzer software (Media

Cybernetics Co.), and the association between snails and the surrounding RGB value was analyzed using a Pearson correlation.

Shell coloration of early postmetamorphic and small juveniles of *C. concholepas* were measured in specimens metamorphosed from competent pelagic larvae. During October 2006, competent larvae (≈1,700–1,900 μm) were caught from the near shore plankton and induced to metamorphose and grow in the laboratory using prey showing contrasting external coloration and commonly present in rocky intertidal habitats where natural settlement of *Concholepas* takes place (35–38). The mussel *P. purpuratus* and the barnacle *N. flosculus* were used as dark and light colored prey items respectively. Metamorphosis and growth were induced and specimens reared under a single prey item. Additionally, both prey items were provided simultaneously (mix diet) during the metamorphosis and the entire rearing phase (28 days). During the rearing, the sizes of offered prey ranged from *ca.* 1 to 3 mm for mussels and 2 to 4 mm for barnacles. Metamorphosis and generation of new teloconch in *C. concholepas* only takes place after prey is accessible (35–37).

To test for shell color plasticity, metamorphosis and the initial growth phase (1–7 days) was induced and supported by a single prey item; then the diet switched to the contrasting colored prey during the final growth phase (8–28 days). After metamorphosis, individuals were maintained in running seawater inside perforated plastic boxes and fed ad libitum. To assess differences in shell color of snails reared under the single, mix and switched diets, the coloration of the newly generated shell was measured on the second day and then regularly at weekly intervals. During October 2008, recently settled individuals (≈1,400–1,700 μm) were collected in El Way, at Antofagasta (23°45′ S, 70°26′ W) and assigned individually to plastic rearing boxes according to one of the following four treatments in which growth was supported by a single prey item; the mussel *S. algosus* ($n = 6$) or barnacle stands of *Jehlius cirratus* and *N. scabrosus* ($n = 6$) representing dark and light colored prey item, respectively. To test for color plasticity, two further treatments ($n = 6$) were applied.

After the initial growth phase (1–28 days) with one prey item the diet was switched to the contrasting colored prey for a final phase of 29–56 days. Periodic photographic records of the shell color, at the growing edge, were made on days 0, 7, 14, 28, 35, 42, 48, and 56. Individual boxes housing the experimental specimens were maintained in running seawater and feed ad libitum with the corresponding prey items. In both experiments the snail shells were prepared for photography by wiping off the excess water and the coloration measured from digital photographs taken with an Olympus C5060WZ digital camera. To detect variations in shell color, we used RGB analysis. The growing edge of snails with a peristomal length ≤ 5 mm were photographed by mounting the camera on an Olympus SZ 51 stereomicroscope. However, the growing edge of snails larger than 5 mm were photographed with the camera set for macro operation with a focal length of 25 mm and a shutter speed of between 1/15 to 1/30 of a second. Pictures were stored in a 2,592 × 1,944 pixel format. From each picture, using Image-Pro 6.2 analysis software, the RGB values at 750 (first experiment) and 250 (second experiment) sampling points over the shell surface were acquired. All sampling points were located within the surface of shell generated during last week of rearing, parallel to, and within 1 mm of, the growing margin of the shells. Average color values were analyzed as repeated measures ANOVA, with diet as fixed factor and the repeated measure being the individual snail over time. Similar results were found in averaged and separated RGB values, so we present results based on averaged RGB values. Differences in size and daily growing rates among treatments were compared by one-way ANOVA with Tukey test as post-hoc comparison.

In the mid-rocky intertidal of central Chile the crab *Acanthocyclus hassleri* prey on barnacles, mussels and small *C. concholepas* (12, 13). We used this crab to test the effect of cryptic shell coloration on the survivorship of newly metamorphosed and small juveniles of *C. concholepas,* with average peristomal length of 1.73 mm (±0.09 SD) and 16.2 mm (±1.90 SD) respectively. Dark newly metamorphosed snails were collected from the rocky intertidal zone of Calfuco dominated by mussels. However, small dark juveniles were obtained in the laboratory by culturing them from newly metamorphosed fed on *P. purpuratus*.

During 2007, the survival of dark *C. concholepas* was evaluated in the laboratory, under cryptic ($n = 12$) and non cryptic ($n = 12$) backgrounds. Mussel beds of *P. purpuratus* with shell length ranging from 1 to 10 mm and barnacle stands (mainly *N. flosculus*) were used as non cryptic and cryptic backgrounds respectively. Prey density, either mussel bed or rock fragments with barnacles, was sufficient to cover the majority of the base of the boxes. In the experiments, food availability was maintained ad libitum to fulfill the demands of the snails and crabs. Individual snails and crabs were placed individually in 1 L (newly metamorphosed) or 2 L (small juveniles) perforated plastic boxes, and maintained in aquaria supplied with running seawater for 2 weeks after which the final survival was evaluated (score: 1 for snails that survived and 0 for lethal attacks). In the experiments, we used large sized male crabs with similar carapace widths (≈23 mm, $n = 24$), and large enough to crush the offered *C. concholepas*. Binary logistic regression was used to analyze the survival of cryptic and non-cryptic individuals, controlling for the effect of snail body size (i.e., peristomal length). For the range of body size selected, snail survival was not influenced by body size (parameter = 0.119 ± 0.097 SD; Wald-$\chi^2 = 1.515$, $P > \chi^2 = 0.218$).

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