

Blind toads in paradise: the cascading effect of vision loss on a tropical archipelago

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Keywords

vision; foraging strategies; reproductive effort; fitness; behavioral plasticity; Fernando de Noronha.

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Editor: Nigel Bennett

Received 11 November 2014; revised 13 February 2015; accepted 16 February 2015

doi:10.1111/jzo.12233

Introduction

A number of amphibians are among the top 100 invasive species in the world (Lowe *et al.*, 2000; Kraus, 2009). In most invaded sites worldwide, these species have caused environmental disturbances (Lowe *et al.*, 2000; Doody *et al.*, 2009; Kraus, 2009; Francis, 2012; Turvey, 2013). Such impacts include the introduction of foreign lethal pathogens (Schloegel *et al.*, 2012), acoustic niche overlap with native species (Both & Grant, 2012), changes in local food webs (Silva & Ribeiro Filho, 2009; Silva, Ribeiro Filho & Feio, 2011; Leivas *et al.*, 2013) and noise pollution (Kraus & Campbell, 2002; Beard & Pitt, 2012). In some instances, introduced populations may not be perfectly suited to the newly occupied location. In these cases, the alien population either cannot persist at the new location (Clout & Williams, 2009), or persists in spite of some handicaps. The latter case is demonstrated by the Cururu toad (*Rhinella jimi*, Bufonidae) in Fernando de Noronha, off the coast of Brazil. A massive population of these toads has lived, fed and reproduced for about a century on the main island of the archipelago (Olson, 1981; Oren, 1984). Nevertheless, almost half of the tadpoles and adults have externally visible deformities (Toledo & Ribeiro, 2009; Toledo *et al.*, 2014). Although the causes are still unknown, such abnormalities could, for example, be a result of inbreeding caused by

Abstract

On the archipelago of Fernando de Noronha, nearly half of the individuals in the invasive population of Cururu toads have mouthpart, limb or eye deformities. Among these, a subset of adult toads is completely blind or has just one functional eye. In this study, we examined the consequences of this vision loss in relation to feeding and reproductive biology. Blind toads were handicapped relative to normal toads, whereas the half-blind individuals were intermediate. In contrast to the expected active hunting mode used by normal toads, blind toads searched for prey using a sit-and-wait foraging strategy. The small sample of blind toads ($n = 4$) had no stomach contents. However, eight half-blinded and 86 sighted animals presented stomach contents, and differed in general diet profile. Body condition as well as reproductive effort increased according to the number of functional eyes. Therefore, we suggest that shifts in feeding and hunting, as a consequence of vision loss, influence diet, with subsequent impact on overall body condition and reproductive effort. A cascade effect of this kind has not been previously reported and provides insightful data related to behavioral plasticity and reproductive fitness.

founder effects, or a consequence of the presence of chemical pollutants in the surrounding environment (e.g. Bacon *et al.*, 2013). Among these, about 20% of adults have eye disorders or malformations, resulting in blind individuals that completely lack functional eyes or half-blind individuals that have just one functional eye (Fig. 1; Toledo & Ribeiro, 2009).

Sight is an important sense in anurans, and its loss can impact several aspects of their ecology and natural history (Ingle, 1976). For example, the foraging strategy of bufonids is often based on active search for prey (Toft, 1980, 1981). Although they may also use other senses, such as olfaction (Alexander, 1965; Shinn & Dole, 1979; Rossi, 1983), hearing (Jaeger, 1976) or touch (Comer & Grobenstein, 1981), most species rely solely on visual cues for prey location, identification, approach and subjugation (Ingle, 1976; Nishikawa, 2000). Furthermore, anurans can modulate their feeding behavior in response to visual analysis of potential prey, increasing feeding success (Anderson & Nishikawa, 1996; Valdez & Nishikawa, 1997). Therefore, the diet of normal, half-blind and blind toads should differ as a consequence of vision loss.

In turn, feeding success contributes directly to vital facets of the individual's biology, including providing sufficient energy and nutrients for the maintenance of basal metabolic rates and growth (Feder & Burggren, 1992; Hillman *et al.*, 2009) and



Figure 1 Normal (a), half-blind (b) and blind (c) *Rhinella jimi* adult toads from the Atlantic ocean archipelago of Fernando de Noronha, state of Pernambuco state, Northeastern Brazil.

reproductive success. Anuran reproductive activities demand high-energy expenditures. For example, calling for female attraction (Toledo *et al.*, 2014) is one of the most costly behaviors among ectothermic vertebrates (Prestwich, Brugger & Topping, 1989; Wells & Taigen, 1989; Gerhardt, 1994), and egg production can utilize almost half of the female caloric content (Smith, 1976). Therefore, with more efficient food (prey) acquisition and selection of high-quality food items, more energy can be invested in reproduction (Schoener, 1971; Lemon, 1991; Wiersma & Verhulst, 2005). In addition, body size and mass are directly correlated with reproductive success of males that are under female selection (Wells, 1977, 1979, 2007). Generally, females choose the nearest larger males (for examples with bufonids, see Wilbur, Rubenstein & Fairchild, 1978; Howard, 1988). Larger males tend to win physical combats as well (reviewed in Shine, 1979), which could be essential to defending a calling or egg-laying site. Size and body mass are also correlated with female breeding success (Bastos & Haddad, 1996), with larger females producing larger numbers of eggs (Davies & Halliday, 1977; Tejedo, 1992; Duellman & Trueb, 1994; Pombal & Haddad, 2005; Wells, 2007). Hence, feeding success affects individuals' size and mass, ultimately influencing reproductive fitness.

Consequently, if the degree of vision loss in Cururu toads affects their foraging behavior and hunting success, we should expect downstream consequences on body condition and reproductive fitness of the invasive population at Fernando de Noronha. We hypothesized that blind individuals would make use of alternative foraging strategies and that blind toads would be handicapped relative to normal ones in terms of food intake, body mass and any measurement of reproductive effort. Additionally, we expected that single-eyed toads present an intermediate condition when compared with normal and completely blind individuals. The archipelago of Fernando de Noronha provides a singular natural laboratory to test these cascade effects, linking natural history, ecology, invasion biology and conservation.

Methods

Feeding behavior

Experiment

We conducted experimental trials to observe how completely blind toads (lacking functional eyes; Fig. 1c) locate and

capture prey in comparison with normal toads (with two normal eyes; Fig. 1a). Therefore, 21 toads (10 blind and 11 normal) were collected in the archipelago of Fernando de Noronha. Half-blind toads (lacking one functional eye; Fig. 1b) were not tested in this trial. Toads were kept in terraria and food was withheld for three consecutive days. After that, they were provided with four adult crickets (collected in the field in the same day of the experiment) and their feeding behavior was recorded with a digital video camera (Sony HandyCam DCR-SR47, Tokyo, Japan) overnight (from 11:00 PM to 07:00 AM).

Feeding trials were performed in a cardboard box (30 × 50 × 40 cm height), which had one wall made of glass to allow film recording. Trials were conducted in an acclimatized room (air temperature near 25°C) with artificial illumination. After the trial, each toad was released in the same location where it was collected. We analyzed the videos with Picture Motion Browser (PMB – Sony). We adopted the methods of all occurrences sampling to qualify behaviors, and sequence sampling to quantify behaviors (Altmann, 1974; Lehner, 1996; Del-Claro, 2004). We recorded the number of attempts to capture prey, how many were successful, if the cricket touched or did not touch the toad before each predation attempt and if so, the number of times the cricket touched the toad.

Statistics

To compare the number of attempts to capture prey, and the proportion of successful attempts during video trails, we did two *t*-tests, with blindness as the independent variable and the dependent variables being number of attempts to capture prey and arcsine-transformed proportion of successful attempts (Zar, 1999).

Diet profile

Field sampling

Collecting was carried out on the archipelago of Fernando de Noronha, Pernambuco, Brazil, during January 2009 and May 2010. We collected 161 toads (76 adult males, 47 adult females and 38 juveniles), of which 143 were normal (two functional eyes), 14 half-blind (only one functional eye), and four blind (no functional eyes), on the main island of the archipelago. We killed the toads with a lethal dose of sodium thiopental injection into the brain through the foramen magnum on the same night of collection, removed the stomachs and fixed them in 10% formalin. The toes of an additional 18 *R. jimi* (6 normal, 6 blind, and 6 half-blind toads) were removed and frozen at –20°C for stable isotope analyses.

Stomach contents

Stomach contents were identified in the lab under a stereomicroscope. The items were identified to the level of order or better. We calculated the volume of each category of prey found in each stomach by means of the alcohol displacement

method (e.g. Phelps *et al.*, 2007). We used the index of relative importance (IRI; Pinkas, Oliphant & Iverson, 1971) to describe the importance of each prey type, combining data on number, volume and occurrence of prey. This was calculated according to the formula: $IRI_t = (PO_t) \times (PI_t + PV_t)$, where PO_t is the percentage of occurrence ($100 \times$ number of stomachs containing item t /total number of stomachs), PI_t is the percentage of individuals ($100 \times$ total number of individuals of t in all stomachs/total number of individuals of all taxa in all stomachs), and PV_t is the percentage of volume ($100 \times$ total volume of individuals of t in all stomachs/total volume of all taxa in all stomachs).

We analyzed the trophic diversity using the standardized Simpson's reciprocal index: B/n , where $B = 1/\sum P_i^2$, where P_i is the proportion of the i th prey item in the sample, and n is the total number of different resources (Pianka, 1973). The dietary overlap among groups was evaluated using the Pianka index (Pianka, 1973): $O_{jk} = Okj = [\sum(p_{ij} \times p_{ik})] / (\sum p_{ij}^2 \times \sum p_{ik}^2)^{0.5}$, where p_{ij} and p_{ik} are the proportion of resource i used by the j and k categories of toads.

Stable isotopes

The previously frozen toes were dried in a greenhouse at 60°C for 48 h. After that, they were triturated and weighed, and approximately 1 mg was placed in specific capsules for analysis. The relative abundances of ^{13}C and ^{15}N were determined at the Centro de Energia Nuclear, Agricultura, Universidade de São Paulo (CENA/USP), Brazil. Samples were analyzed in a Micromass 602E mass spectrometer (Finnegan Mat, Bremen, Germany).

Statistics

We used t -tests to compare number and volume of prey between half-blind and normal toads (blind toads in our sample contained no food items). Changes on diets among groups were evaluated by G -tests using IRIs. We compared isotopic composition between normal, half-blind and blind toads using analyses of variance (ANOVAs). We tested homogeneity of variances and normality prior to performing the analyses, and transformed the data when necessary. Differences were considered significant when $P < 0.05$ (Zar, 1999).

Body condition and reproductive effort

To test the hypothesis that blind toads are handicapped in relation to normal ones in traits associated with feeding, we collected blind, half-blind (one-eyed toads) and normal toads in Fernando de Noronha and killed them (as described above). After that, we weighed, measured the snout-vent length (SVL) and did necropsies in adult toads to remove gonadal adipose tissue (of both sexes) and female ovaries. Female ovaries were weighed and the number of oocytes was estimated. To achieve this, we weighed the ovaries, removed a 3 g subsample, counted the oocytes in the subsample, and used this to estimate the total number of oocytes in the ovaries. SVL was measured to the nearest 0.1 mm using a digital

caliper, and weight was recorded to the nearest 0.05 g using compact field scales. Body mass was calculated considering the adipose body mass and egg mass as covariables. Reproductive effort was calculated as the ratio of clutch to liquid body mass (i.e. without ovaries mass; see Prado, Uetanabaro & Lopes, 2000).

Statistics

Data on physical conditions of blind, half-blind and normal toads were analyzed using analysis of covariance, after log-transforming all variables: liquid body mass (total body mass subtracted by the ovaries mass), SVL, gonadal tissue mass and number of eggs produced. Females without eggs in their gonads were not included in the analyses. As there were no significant effects of body mass or SVL on the number of eggs produced (Supporting Information Fig. S1), we opted to run an ANOVA to compare reproductive effort (which already takes body mass into account) of blind, half-blind and normal females.

Before all analyses, we performed Levene's tests of homogeneity of variance and visually analyzed normality. When necessary, data were transformed according to the recommendations of Zar (1999).

Results

Feeding behavior

We observed four different behaviors in the predators (toads): (1) moving toward a prey; (2) attempting to capture a prey by tongue projection; (2) immobility; and (4) pushing the prey away, when it was on the toad. For the prey (crickets), we observed three different behaviors: (1) moving in front of the predator; (2) touching the predator; and (3) fleeing from the predator. These behaviors followed an escalated order as presented in Fig. 2.

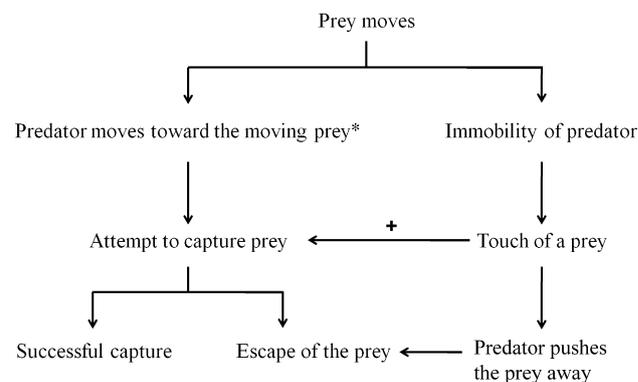


Figure 2 Ethogram based on observed behaviors exhibited by the predators (common toads from Fernando de Noronha, Brazil) and its prey (crickets) during the experimental trials. *Behavior not observed in blind toads; +behavior not observed in normal toads.

Table 1 Predation strategy, efficacy and diet profile of three sight conditions (normal, half blind and blind) of common toads (*Rhinella jimi*) from Fernando de Noronha, Brazil

		Sight condition		
		Normal	Half blind	Blind
Predation strategy	Main sense used for predation	Visual	NA	Tactile
Predation efficacy	Number of attempts to capture prey	14.36 ± 2.07 (5–27; 11)	NA	4.00 ± 1.40 (0–11; 10)
	Percentage of successful attempts	22.82 ± 5.37 (5.26–66.67; 11)	NA	22.02 ± 10.30 (0–100; 10)
Stomach contents	Number of prey items	72.64 ± 11.26 (1–547; 89)	27.75 ± 14.05 (1–122; 8)	NA
	Volume of prey items (cm ³)	1.99 ± 0.36 (0–19; 89)	0.57 ± 0.26 (0–1.7; 8)	NA
	Fast motion prey	92	61	NA
	Slow motion prey	6	37	NA
	Motionless prey	2	1	NA
	Aquatic prey	0	1	NA

Number of attempts to capture prey, percentage of successful attempts, number and volume of stomach contents [presented as mean ± standard error (range; sample size)], numeric frequency (presented as percentage of IRI) of the different prey types classified according to their generalized locomotion pattern. NA, not available.

Feeding behavior was different between blind and normal toads. Normal toads behaved as active foragers using vision exclusively to locate their prey (Supporting Information Video S1). Blind toads behaved as sit-and-wait predators, and located their prey by means of tactile stimuli exclusively (Supporting Information Video S2). Crickets touched each blind toad 31.25 (±32.90) times and each normal toad 0.64 (±1.03) times on average. Blind toads were successful in capturing the prey in 39 out of the 40 attempts. None of the 158 attempts of the normal toads to capture the crickets occurred after tactile stimulation by the cricket (Supporting Information Table S1).

Blind toads had fewer prey capture attempts than normal ones ($t_{19} = -4.6$, $P < 0.001$; Table 1), but the proportion of successful attempts did not differ between blind and normal toads ($t_{16} = 1.39$, $P > 0.1$; Table 1).

Diet profile

Eighty-six normal (62%), eight half-blind (57%) and none of the blind toads had identifiable stomach contents. We identified 28 prey categories, 27 of them invertebrates and one vertebrate (the endemic lizard *Trachylepis atlantica*; Supporting Information Table S2). Ants (Hymenoptera) and Coleoptera occurred in a large proportion of stomachs in both normal and half-blind toads. All prey categories were present in at least one normal toad stomach, and 14 of them were observed in half-blind toad stomachs (Supporting Information Table S2). The number and volume of prey items per stomach were not significantly different between normal and half-blind toads (number: $t_{95} = -1.27$, $P = 0.21$; volume: $t_{95} = -1.64$, $P = 0.10$; Table 1). However, diet composition, considering the IRI, showed significant difference among the two toad classes ($G = 95.4$, d.f. = 27, $P < 0.001$; Table 1). The trophic diversity was 0.12 in normal toads and 0.31 in half-blind toads, and the trophic niche overlap between them was 0.35.

Normal toads contained larger numbers of Coleoptera and ants, whereas half-blind toads had more termites (Isoptera) and Diplopoda. Normal toads also had a greater relative volume of Coleoptera and pupae of *Musca* sp. (Diptera), whereas half-blind toads contained more Diplopoda and Coleoptera. All toads primarily fed on fast-moving organisms, but half-blind individuals also contained a large proportion of slow-moving prey (Table 1).

Relative frequencies of stable isotopes did not differ between groups ($\delta^{15}\text{N}$: $F_{2,15} = 1.63$; $P = 0.23$; $\delta^{13}\text{C}$: $F_{2,15} = 1.55$; $P = 0.24$; Fig. 3), but the difference was marginally non-significant ($\delta^{15}\text{N}$: $t = -1.86$; $P = 0.08$; $\delta^{13}\text{C}$: $t = -1.81$; $P = 0.09$) when comparing normal and all deformed toads combined. The trend observed was that blind and half-blind toads were higher in ^{13}C and ^{15}N relative to normal ones.

Body condition and reproductive effort

Blind toads had smaller liquid body mass in relation to their size than normal individuals, and half-blind toads were intermediate ($r^2 = 0.71$, $P < 0.01$; $F_{2,235} = 3.47$, $P = 0.03$, Supporting Information Fig. S2). The gonadal adipose tissue of adults did not differ between blind, half-blind and normal toads ($F_{2,50} = 0.29$, $P > 0.05$; Supporting Information Fig. S1).

The mean number of oocytes produced per female was $25\,271 \pm 12\,744$ (range: 3540 to 51 012; $n = 27$). The number of oocytes produced, although nearly significant, was not correlated to female liquid body mass ($r^2 = 0.13$; $P = 0.07$; $n = 19$; Supporting Information Fig. S1) neither to SVL ($r^2 = -0.04$; $P = 0.56$; $n = 19$). However, the number of oocytes produced differed between the groups of toads with different numbers of functional eyes ($F_{2,22} = 3.69$; $P = 0.04$). Similarly, reproductive effort differed between groups ($F_{2,14} = 9.998$; $P = 0.007$; Fig. 4). In both cases, the trend was the same: the number of

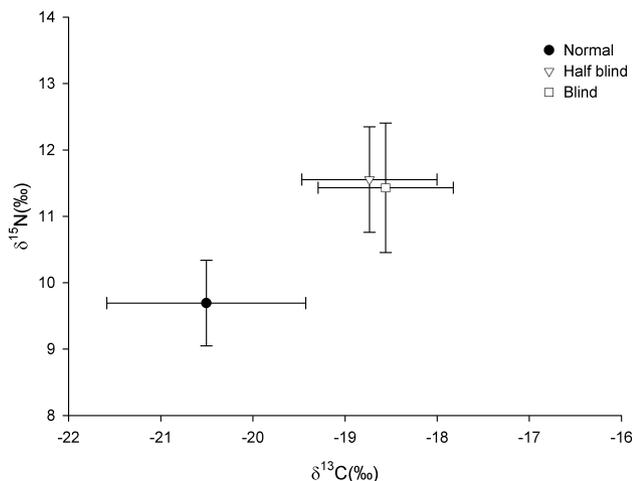


Figure 3 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures of normal (black), half-blind (gray), and blind (white) common toads from Fernando de Noronha, Brazil. Bars represent standard errors.

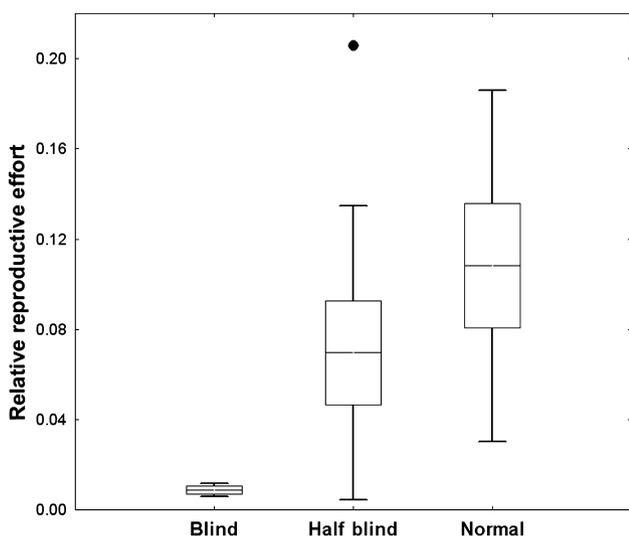


Figure 4 Reproductive effort of the three functional groups (blind, half blind and normal sighted) of *Rhinella jimi* from Fernando de Noronha. Line inside the box indicates the mean, boxes represent the standard error, whiskers indicate the standard deviation and the dot is an outlier.

eggs or reproductive effort increased with number of functional eyes (Fig. 4).

Discussion

Our study revealed a cascade effect from feeding behavior to reproduction in an introduced toad population in Brazil (Fig. 5). As we observed, predation strategies employed by normal and blind toads are opposite: active versus sit-and-wait forager; visual versus tactile cues. Such behavioral plas-

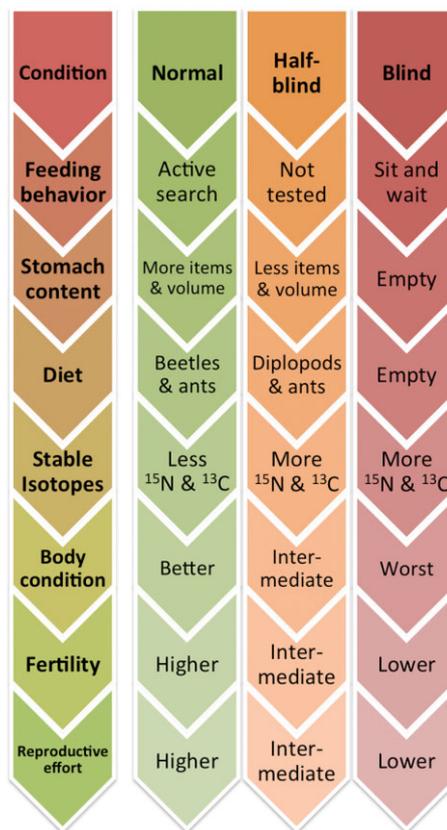


Figure 5 Diagram of the cascading effect of losing one (orange column) or both eyes (red column) in comparison to normal toads (green column). Sight depletion forces animals to modify their foraging strategy (active searching based on vision to sit-and-wait based on touch), which causes differences in their prey intake and diet (indicating the most relevant prey items), generating different stable isotopes profiles, leading to differences in body condition (a relationship between body size and mass), ultimately reducing the female fertility (number of ovules produced) and reproductive effort (a relationship between size/mass and ovules produced).

ticity is an amazing example of amphibians' ability to adapt to adverse conditions, which could be deleterious for many vertebrates in natural systems. This could help to explain how blind and otherwise deformed toads are able to persist in equal numbers as normal individuals in Fernando de Noronha (Toledo & Ribeiro, 2009).

According to the optimal foraging theory, animals should select the best diet based on associated energetic costs (MacArthur & Pianka, 1966; Schoener, 1979). Prey selection also depends on relative abundance of prey items in the habitat and on traits of each prey item, such as size, shape, motion direction and speed (Valdez & Nishikawa, 1997). Bufonids are usually active hunters (wide foraging, *sensu* Pianka, 1966), feeding mainly on small prey items that they encounter during their foraging activity in relatively large areas (Toft, 1980). Predators using tactile cues to locate prey

are probably unable to perceive either prey abundance or morphological traits before capturing them (Duellman & Trueb, 1994). As blind toads are unable to discriminate abundance, size, shape and any other visually detectable traits of their prey, we suggest that they will eat any touched prey and are unable to select an optimal diet, as normal ones should be. Furthermore, as we did not observe tactile hunting in normal toads, we suggest that it should be disadvantageous relative to visual hunting. This advantage would be in regard to food selection, individual feeding specialization and feeding efficacy (e.g. hunting more profitable prey in less time).

As a result, this behavioral change could have led to a different diet profile between blind, half-blind and normal toads. We suggest that it affected the frequency of food acquisition and the prey types consumed; for example, fast-moving prey, which are more difficult to capture, were more common in the stomachs of normal toads (Table 1). Trophic diversity was low for both (half-blind and normal) toad groups, and was greater in half-blind toads. This could be explained by higher evenness among the IRIs of different prey types consumed. The degree of niche overlap between half-blind and normal toads was low (0.35 in a scale that varies between 0 and 1), corroborating the differences in diet composition.

Among the prey items, two species recorded in the diet of *R. jimi* from Fernando de Noronha deserve special attention: the crab *Johngarthia lagostoma* (Decapoda, Gecarcinidae), endemic to oceanic islands (Ascension Island, England; and Trindade, Fernando de Noronha, and Atol das Rocas, Brazil; Hartnoll, Mackintosh & Pelembe, 2006) and endangered in Brazil, mainly as a consequence of habitat loss and hunting pressures (Machado, Drummond & Paglia, 2008); and the skink *Trachylepis atlantica* (Squamata, Scincidae, Lygosominae), endemic to Fernando de Noronha, and representing the most western geographic record for the genus (Mausfeld *et al.*, 2002). The predation of such endemic and endangered fauna highlights the possible negative impacts of this human-introduced species on the biodiversity of oceanic islands, which are more vulnerable to invasions (Lowe *et al.*, 2000). Besides this skink, previous reports on the diet of adult *R. jimi* included the presence of other vertebrates as prey items, such as congeneric toads (Guix, 1993; Chaves, Oliveira & Moura, 2012) and bats (Gouveia *et al.*, 2009; Silva, Santos & Amorim, 2010).

While for recently metamorphosed individuals, dipterans and ants were the most important prey items (Brito & Cascon, 2012); for normal adult toads, coleopterans and ants were the most important items. Therefore, dipterans seem to be replaced by coleopterans in the adult diet, probably because of their larger size, and consequently higher energetic budget. Ants, on the other hand, remain as a relatively important item, probably because of their great abundance in terrestrial environments, in many cases representing the largest animal biomass available (Fittkau & Klinge, 1973; Krüger & McGavin, 1998).

The proportion of ^{15}N in tissues normally reflects trophic relations and increases with trophic level (Minagawa & Wada, 1984), suggesting that deformed toads feed on more carnivorous prey than normal toads. However, starving animals also

show increased values of ^{15}N (Hobson, Alisauskas & Clark, 1993), suggesting that deformed individuals may have poor body condition. Half-blind toads contained a large number of Diplopoda, but this cannot explain the differences in $\delta^{15}\text{N}$ because these invertebrates are typically saprophagous (Hopkin & Read, 1992) and low in ^{15}N (e.g. Scheu & Falca, 2000). We suggest that the difference observed in $\delta^{15}\text{N}$ reflects the difficulty of eye-deformed toads in obtaining food. Further evidence that the diet of normal toads differs from that of blind and half-blind toads comes from measurements of ^{13}C . Plants with C_3 metabolic pathways have lower proportions of ^{13}C than do C_4 plants (Smith & Epstein, 1971; Post, 2002), and this is reflected in the tissues of consumers. Blind and half-blind toads in our sample are part of food webs based more on C_4 plants than are normal toads, perhaps because of sensory-induced differences in foraging strategies.

Although all classes of toads (deformed or normal) can feed in the archipelago, we observed an increasing weakening of body condition with increasing deformity severity (Supporting Information Fig. S2). We hereby postulate that it could be a consequence of the sit-and-wait plus tactile sense strategy employed by blind toads, as this might provide fewer meals than the active foraging plus visual prey selection strategy. This suggestion is corroborated by the observed increase in stomach contents from blind to normal toads (Table 1).

Individual fitness is influenced by body mass in several ways. Usually, smaller and lighter males mate fewer times than larger ones (Bastos & Haddad, 1996) and they are more likely to lose aggressive interactions, such as territorial fights, scrambles for females and attempts to dislodge amplexant males, which are common behaviors among explosive breeders (Wilbur *et al.*, 1978; Arak, 1983; Bastos & Haddad, 1996; Toledo & Haddad, 2005). Smaller and lighter females are also handicapped because the body mass of a female is usually positively correlated to egg production (Berven, 1988; Bastos & Haddad, 1996; Prado & Haddad, 2005). Accordingly, we observed that the number of functional eyes was correlated to the number of eggs produced. Therefore, it is possible that feeding biology among the different groups ultimately impact reproductive effort (Fig. 5).

The present study demonstrated differences in the foraging behavior and diets of normal and deformed toads. These different life-history traits may, in turn, influence size, mass and ultimately impact reproductive fitness (Fig. 5). Although artificial, in the sense of an introduced and invasive population, our study provides evidence of innate behavioral plasticity, and resilience to adverse morphological conditions (with unknown origins), which even native non-invasive populations face. Unusual cases of blindness have also been observed in other toads (Bacon *et al.*, 2013) and snakes (Wharton, 1969; Bonnet *et al.*, 1999) introduced on islands. In these cases, some environmental similarities can be highlighted, such as the indication of a predator-free environment, and the presence of abundant, sessile or slow-moving prey. Furthermore, these vertebrates also share some intrinsic characteristics, such as the presence of highly toxic secretions, a sit-and-wait predatory strategy and a generalist diet (Table 2). Therefore, it seems that a particular set of environmental conditions and

Table 2 Traits present in the environment or in wild populations of terrestrial blind vertebrates introduced in islands

Species (common name) Reference	Environment					Animal					
	Introduced in island	Predator-free environment	Abundant food items	Sessile or slow motion prey	Highly toxic or poisonous	Generalist diet	Rely on different sensory modalities	Plasticity to survive in the newly invaded environment	Sit-and-wait predator	Blindness affects fitness	Cause of blindness
<i>Rhinella jimi</i> (common toad) Toledo & Ribeiro 2009	Y	Y	Y	Y*	Y	Y	Y	?	Y*	Y	?
<i>Rhinella marina</i> (cane toad) Bacon <i>et al.</i> , 2013	Y	Y	Y	?	Y	Y	Y	?	?	?	Chemical pollutants
<i>Notechis scutatus</i> (tiger snake) Bonnet <i>et al.</i> , 1999	Y	Y	Y	Y	Y	Y	Y	Y	Y	No	Gulls attack
<i>Agkistrodon piscivorus</i> (cottonmouth viper) Wharton 1969	Y	Y	Y	Y	Y	No	Y	?	Y	No	?

An asterisk ** indicate a condition exclusively observed in blind individuals. Y = yes; No = no; ? = unknown.

animal traits is necessary to allow the persistence, and occasionally the evolution of blind vertebrates.

Acknowledgments

We thank Allan Pessier, Michael J. Lannoo, Gad Perry and Anat Belasen for reviewing the English and for providing insightful suggestions to the manuscript; E. Silva, M. Navarro, R. Ribeiro and V. Fernandes for assistance in the field; M. Araújo and R. Oliveira for helping with the isotopic analyses. Allan Pessier also provided the picture of the half-blind toad. Research and collecting permit (17242-1) was provided by *Instituto Chico Mendes de Conservação da Biodiversidade* (ICMbio). Funding was provided by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP: 2008/50325-5 and 2008/52847-9 to L.F.T. and 2009/03736-2 to J.T.), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES: 2009/03736-2 to J.T.) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq: 405285/2013-2 and 302589/2013-9 to L.F.T.).

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Relationships between body mass and gonadal adipose tissue (a); and clutch size (b) of normal (closed circles), half-blind (open circles) and blind individuals (triangles) of common toads from Fernando de Noronha, Brazil.

Figure S2. Relationships between body mass and size (snout-vent length) in normal (black, dashed line), half-blind (gray, dotted line), and blind (white, solid line) individuals of common toads from Fernando de Noronha, Brazil. Both axes were natural log transformed.

Table S1. Attempts to capture prey, successful attempts and stimuli before attempts. Observed during each video trial with adults of common toads from Fernando de Noronha, Brazil.

Table S2. Numeric frequency, volumetric frequency, frequency of occurrence and proportion of index of relative importance (Pinkas *et al.*, 1971) of different prey types found in the stomachs of normal and half-blind common toads from Fernando de Noronha, Brazil.

Video S1. Normal toad preys on cricket.

Video S2. Blind toad preys on cricket.