Herpetological Conservation and Biology 10(2):661–665.
Submitted: 24 December 2014; Accepted: 17 June 2015; Published: 31 August 2015.

FLIGHT INITIATION DISTANCES OF *TROPIDURUS HISPIDUS* AND *TROPIDURUS SEMITAENIATUS* (SQUAMATA, TROPIDURIDAE) IN SYMPATRY

THIAGO MAIA-CARNEIRO[1] *AND CARLOS FREDRICO D. ROCHA*

Departamento de Ecologia, Universidade do Estado do Rio de Janeiro, Rua São Francisco Xavier 524, CEP 20550–013, Rio de Janeiro, Brazil
[1]Corresponding author, e-mail: tmaiacarneiro@gmail.com

***Abstract*.—Flight initiation distance (FID) is the minimum approach distance allowed for a potential predator before an animal starts a locomotor escape. Factors such as body size and body temperature might affect this behavior in lizards. Here, we analyzed the influences of these factors on defensive behaviors of sympatric lizards *Tropidurus hispidus* and *T. semitaeniatus* on rock outcrops in northeastern Brazil. All individuals of the two species employed locomotor escape. Shorter FID for *T. semitaeniatus* in comparison with *T. hispidus* suggested that the former rely more on immobility to conceal their presence and/or that it is more effective at evading predators. Furthermore, *Tropidurus hispidus* lizards might be faster than *T. semitaeniatus* and because of that, individuals may take flight early at low velocities and retain the capacity to increase their velocity when necessary. Inter-specific differences in body dimensions apparently represented important influences for this defensive behavior. Neither SVL nor body mass were important factors influencing intra-specific variations in FID. At low body temperatures, *T. hispidus* tended to exhibit greater FID, presumably due to impaired locomotor capacity.**

Key Words.—anti-predator behavior; approach distance; defense behavior; defensive mechanisms; escape behavior

INTRODUCTION

Lizard prey may permit a minimum approach distance for a predator before starting a locomotor escape for capture avoidance, which is the flight initiation distance (FID; Ydenberg and Dill 1986; Cooper and Frederick 2007), and body size, body temperature, and differences in escape efficiency might influence this behavior. For instance, in North America, *Callisaurus draconoides* had lower FID compared to *Cophosaurus texanus* possibly due to its greater body dimensions that make it more visible to predators and/or to differential energetic constraints (Bulova 1994). In Brazil, *Tropidurus oreadicus* with low body temperatures had longer FID than individuals with higher body temperatures (Rocha and Bergallo 1990). For related sympatric species co-occurring locally, escape decisions might be qualitatively similar due to relatedness, and divergences in defense responses (e.g., in FID) might arise from inter-specific ecological differences that affect prediction of risk (Cooper and Avalos 2010).

The lizards *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata, Tropiduridae) often occur in sympatry on rock outcrops in northeastern Brazil. *Tropidurus hispidus* occurs in several ecoregions along its broad geographic distribution range in South America, inhabiting Amazonian savannas, Atlantic Forest, Cerrado, and Caatinga (Rodrigues 1987, 1988; Avila–Pires 1995; Carvalho 2013). *Tropidurus semitaeniatus* occurs in Caatinga, Cerrado boundaries, and in zones towards the Atlantic Forest, where it is found primarily on rock outcrops (Carvalho 2013).

Morphological differences exist between *T. hispidus* and *T. semitaeniatus*: individuals of the former species are bulkier and achieve larger body sizes, whereas the latter are flattened and smaller, allowing them to take refuge in relatively narrow crevices (Vitt 1981, 1993; Vitt and Goldberg 1983, but see Vitt et al. 1997). In this context, one would expect the occurrence of inter-specific differences in FID influenced by differences in body dimensions. Here, we investigate influences of body size (snout-vent length and body mass) and body temperature on FID exhibited by *T. hispidus* and *T. semitaeniatus* lizards, considering possible inter and intra-specific variations. We hypothesized that lizards that are more visible should run earlier in face of a potential predator and that low body temperatures may result in longer FID. Otherwise, larger lizards could have shorter FID due to greater ability to escape in high speeds.

MATERIALS AND METHODS

***Study area.*—**We collected data in rock outcrop areas in Igatu, in the municipality of Andaraí, state of Bahia, northeastern Brazil (12°53'S, 41°19'W), in the surroundings of the Parque Nacional da Chapada Diamantina. Overall, due to particular altitudinal

Copyright © 2015. Thiago Maia-Carneiro
All Rights Reserved

TABLE 1. Snout vent–length (SVL, mm), body mass (g), body temperature (T_b, °C), and flight initiation distance (FID, cm) of *Tropidurus hispidus* and *T. semitaeniatus* in Igatu, municipality of Andaraí, state of Bahia, Brazil. Values are presented as mean ± standard deviation. The range and number of observations are between parentheses.

Species	SVL	Body mass	T_b	FID
Tropidurus hispidus	86.3 ± 19.9 (57.7–133.2; n = 18)	26.1 ± 23.1 (6.0–90.5; n = 18)	36.0 ± 2.2 (30.6–39.2; n = 18)	160.5 ± 69.2 (72.8–282.0; n = 18)
Tropidurus semitaeniatus	57.3 ± 6.3 (44.9–68.7; n = 24)	4.1 ± 1.7 (2.3–7.8; n = 24)	36.1 ± 1.6 (32.6–39.8; n = 25)	92.6 ± 47.0 (22.7–196.7; n = 25)

conditions, the climate is mesothermic of the Cwb type in Köppen's classification (1923), with milder temperatures (annual averages bellow 22 °C) compared to nearby regions (Rocha et al. 2005). The area where we collected data was a semi-arid environment having sand soils occupied by undergrowth and herbaceous and shrubby vegetation, but predominantly covered by rock outcrops.

Data collection and statistical procedures.—We collected data in March 2013 through visual encounter surveys conducted along transects for 30 min at each hour between 0900 and 1700 (total sample effort of 1440 min distributed equally throughout six days). We made slow walks across the area while searching for lizards on the ground, logs, cacti, and stones, as well as on the vegetation. Whenever an individual lizard was sighted, one of the authors (Thiago Maia-Carneiro) moved slowly, straight towards the lizard and, once the lizard moved, marked its initial position and that of the investigator (with scratches on the rocks or with a ribbon tied to a rock). An attempt was then made to capture the lizard by noose or by hand. We encountered all lizards on rocks and mainly at heights up to 1.5 m. We collected captured individuals for a study of feeding habits, which eliminated the occurrence of pseudo-replication.

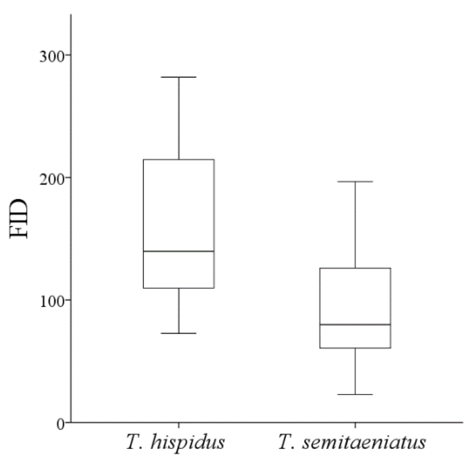


FIGURE 1. Differences in minimum flight initiation distances (FID, cm) between *Tropidurus hispidus* and *T. semitaeniatus* in Igatu.

We measured FID with a tape (to 0.1 cm) as the distance from the potential predator (investigator) to the lizard when the escape behavior started. To control stimulation from the potential predator, the same investigator (TMC) approached lizards in all trials at similar speeds and wore similar clothes (despite evidence that the color of clothing does not influence FID: Cooper and Pérez-Mellado 2011). We recorded the body temperature (T_b) of each captured lizard with a Miller and Weber quick-reading cloacal thermometer (± 0.2 °C precision). We measured snout-vent length (SVL) with a caliper (0.01 mm) and body mass with spring scales (0.25 g for individuals up to 30 g; 1.0 g for heavier individuals). We evaluated possible inter-specific differences in FID, SVL, body mass**,** and T_b between *T. hispidus* and *T. semitaeniatus* using ANOVA (Zar 1999). We used linear regression analyses to assess the importance of SVL, body mass, and T_b on FID of *T. hispidus* and *T. semitaeniatus* (Zar 1999).

RESULTS

Tropidurus hispidus had significantly greater FID than *T. semitaeniatus* ($F_{1, 41}$ = 14.707, P < 0.001; Fig. 1; Table 1). There was no difference in T_b of *T. hispidus* and *T. semitaeniatus* ($F_{1, 41}$ = 0.007, P = 0.935), but individuals of *T. hispidus* were significantly longer ($F_{1, 40}$ = 45.202, P < 0.001) and heavier ($F_{1, 40}$ = 84.957, P < 0.001; Table 1). There was no significant relationship between SVL and FID in *T. hispidus* (r = 0.163, $F_{1, 16}$ = 0.436, P = 0.519) or *T. semitaeniatus* (r = 0.233, $F_{1, 22}$ = 1.265, P = 0.273; Fig. 2; Table 1). Similarly, body mass and FID were unrelated in *T. hispidus* (r = 0.146, $F_{1, 16}$ = 0.348, P = 0.563) and *T. semitaeniatus* (r = 0.145, $F_{1, 22}$ = 0.474, P = 0.498; Fig. 2; Table 1). For *T. hispidus*, FID was negatively related to T_b (r = 0.609, $F = _{1, 16}$ = 9.409, P = 0.007), but this relationship was not significant in *T. semitaeniatus* (r = 0.167, $F_{1, 23}$ = 0.659, P = 0.425; Fig. 2; Table 1).

DISCUSSION

Individuals of *T. hispidus* and *T. semitaeniatus* in Igatu remained immobile as they monitored the predator's approach and then fled when the risk became

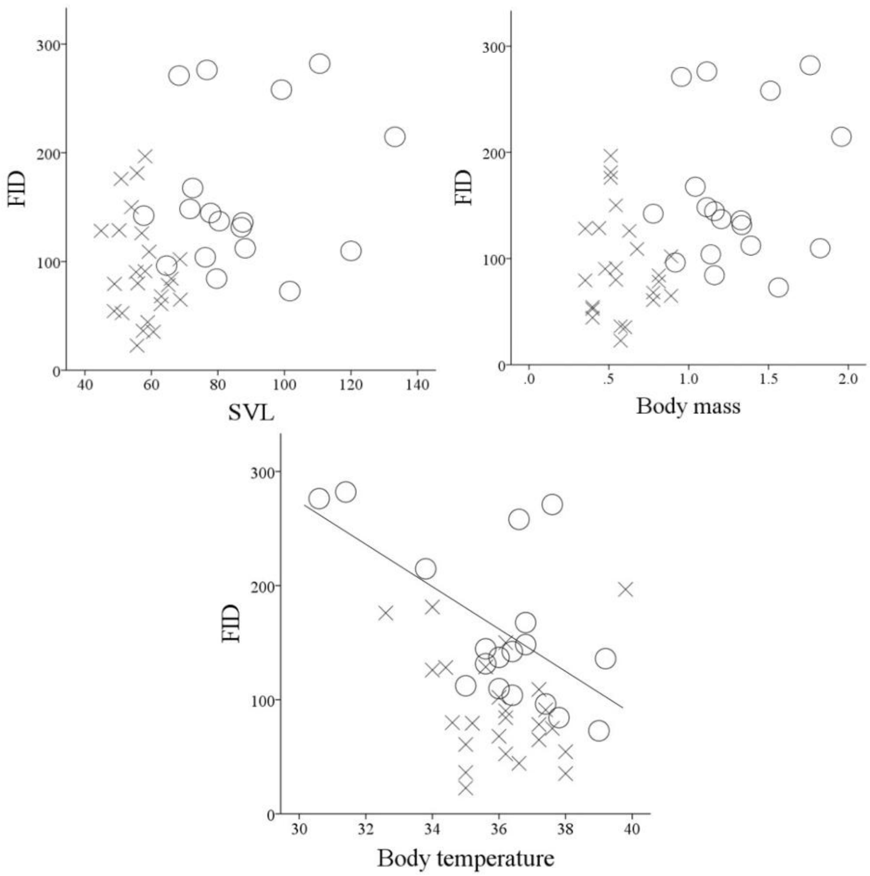


FIGURE 2. Distributions of data regarding (top left) flight initiation distance (FID, cm) and snout-vent length (SVL, mm), (top right) FID and body mass (g, log), and (bottom) FID and body temperature (°C) for *Tropidurus hispidus* (○) and *T. semitaeniatus* (×) in Igatu. The regression line represents the statistically significant relationship between FID and body temperature in *T. hispidus*.

too great to justify continued immobility, matching the scenario of economic escape theory (Ydenberg and Dill 1986; Cooper and Frederick 2007). Predators sometimes detect or attack prey after stimulated by their movement (Greene 1988); thus, remaining motionless might represent an advantage for prey before relying on flight. Immobility was considered important to reduce the chances of lizards *T. montanus* being detected by predators (Machado et al. 2007). Considering that in open environments lizards are more conspicuous to visually oriented predators, defense through immobility potentially increases the chances of survival of these animals in rock outcrops, until the predator is close enough that it is likely to have detected the prey, increasing the risk of capture while fleeing.

The differences in FID between *T. hispidus* and *T. semitaeniatus* in Igatu may have occurred because of influences from body size. This suggestion is consistent with results of a study including over 60 species of lizards in which FID increased inter-specifically as SVL increased (Cooper et al. 2014). Possibly, the larger size of *T. hispidus* might render them more conspicuous and thus more susceptible to predator attacks. Furthermore, the larger size of *T. hispidus* in comparison to *T. semitaeniatus* might render individuals easier to locate after escape and hamper the flight and shelter in small refuges. Indeed, *T. semitaeniatus* has a flattened morphology typical of rock-dwelling lizard species (Vitt et al., 1997; Revell et al., 2007) and is commonly associated with rock crevices that individuals may use as shelter for evading predation (Vitt, 1981, 1993; Vitt and Goldberg, 1983; Ribeiro et al., 2012). In addition, *T. hispidus* lizards might be faster than *T. semitaeniatus* and, because of that, individuals may afford to flight early at low velocities and retain the capacity to increase their velocity whether necessary. In North America, large *Sceloporus woodi* lizards that have greater maximum velocities than smaller individuals attained maximum velocity less frequently during flight and ran early (Stiller and McBrayer 2013). By doing this, larger lizards reduce risks associated to interactions with predators, preserve energy that would be expended during rapid flight, and maintain the ability to flee again if a predator approaches soon after fleeing (Stiller and McBrayer 2013). Nevertheless, the shorter FID for *T. semitaeniatus* in Igatu compared with *T. hispidus* might indicate that these lizards rely more on immobility to conceal their presence and/or that they are more effective at evading predators (e.g., by using rock crevices).

Despite the importance of body size promoting divergences in FID between species in Igatu, intra-specifically, body dimensions were irrelevant based on our analysis. Individuals of different sizes within each species had similar sensibility to predation risk, allowing potential predators to approach similar minimum distances regardless of particular body dimensions. Nonetheless, this similar prediction of risk might have occurred due to the potential predator in this study (a human) have a body size larger than those of more common actual predators of the lizards in the environment, which may have influenced the behavioral responses. Both *T. hispidus* and *T. semitaeniatus* lizards in Igatu used squirreling (running to opposite side of tree or rock) as a defensive strategy, a behavior documented to occur in different lizard species (e.g. Regalado 1998; Smith and Lemos-Espinal 2005), and also fled into burrows after the observer approach. Similar behaviors have been reported for other tropidurid species and are widespread among lizards (Vitt 1993; Vitt and Goldberg 1983; Faria and Araujo 2004; Machado et al. 2007; Meira et al. 2007).

Intra-specifically, *T. hispidus* that had comparatively lower body temperatures tended to have greater FIDs than individuals with higher body temperatures. Body temperature affects the physiological state of lizards and its variation influence defensive responses by these animals. Low body temperatures may impair locomotor performance in lizards (Hertz et al. 1982; Autumn et al. 1994), which in turn may affect predator escape behaviors, with lizards that have low body temperatures running earlier from potential predators than individuals with higher body temperatures (Rand 1964). The inverse relationship between T_b and FID presumably is a compensatory strategy to overcome reduced escape ability at lower body temperatures. Such relationship may have not occurred within *T. semitaeniatus* because of small variations of FID and T_b in comparison with *T. hispidus*, which may influence the detectability by statistical tests.

Acknowledgments.—We thank Daniel Cunha Passos, Gisele Regina Winck, and Vanderlaine Amaral Menezes for the contributions in the manuscript. We thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for providing grants to CFDR (processes n° 304791/2010–5 n° 470265/2010–8 and 472287/2012-5). Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) supported CFDR through the Program "Cientistas do Nosso Estado" (process n° E–26/102.765/2012). Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) granted a Ph.D. scholarship to TMC.

LITERATURE CITED

Autumn, K., R.B. Weinstein, and R.J. Full. 1994. Low cost of locomotion increases performance at low temperature in a nocturnal lizard. Physiological Zoology 67:238–262.

Avila–Pires, T.C.S. 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). Zoologische Verhandelingen 299:1–706.

Bulova, S.J. 1994. Ecological correlates of population and individual variation in antipredator behavior of two species of desert lizards. Copeia 1994:980–992.

Carvalho, A.L.G. 2013. On the distribution and conservation of the South American lizard genus *Tropidurus* Wied–Neuwied, 1825 (Squamata: Tropiduridae). Zootaxa 3640:42–56.

Cooper, W.E., and A. Avalos. 2010. Escape decisions by the syntopic congeners *Sceloporus jarrovii* and *S. virgatus*: comparative effects of perch height and of predator approach speed, persistence, and direction of turning. Journal of Herpetology 44:425–430.

Cooper, W.E., and W.G. Frederick. 2007. Optimal flight initiation distance. Journal of Theoretical Biology 244:59–67.

Cooper, W.E., and V. Pérez–Mellado. 2011. Escape by the balearic lizard (*Podarcis lilfordi*) is affected by elevation of an approaching predator, but not by some other potential predation risk factors. Acta Herpetologica 6:247–259.

Cooper, W.E., R.A. Pyron, and T. Garland. 2014. Island tameness: living on islands reduces flight initiation distance. Proceedings of the Royal Society of London B 281: 20133019. http://dx.doi.org/10.1098/rspb.2013.3019

Faria, R.G., and A.F.B. Araujo. 2004. Sintopy of two *Tropidurus* lizard species (Squamata: Tropiduridae) in a rocky Cerrado habitat in central Brazil. Brazilian Journal of Biology 64:775–786.

Greene, H.W. 1988. Antipredator mechanisms in reptiles. Pp.1–152 *In* Biology of the Reptilia, vol. 16, Ecology B. C. Gans, and R.B. Huey (Eds.). John Wiley and Sons, New York New York, USA.

Hertz, P.E., R.B. Huey, and E. Nevo. 1982. Fight versus flight: body temperature influences defensive responses of lizards. Animal Behavior 30:676–679.

Koppen, W. 1923. Dle Klirnate der Erde. Walter de Gruyter, Berlin, Germany.

Machado, L.L., C.A.B. Galdino, and B.M. Sousa. 2007. Defensive behavior of the lizard *Tropidurus montanus*

(Tropiduridae): effects of sex, body size and social context. South American Journal of Herpetology 2:136–140.

Meira, K.T.R., R.G. Faria, M.D.M. Silva, V.T. Miranda, and W. Zahn-Silva. 2007. História natural de *Tropidurus oreadicus* em uma área de cerrado rupestre do Brasil Central. Biota Neotropica 7:155–164.

Rand, A.S. 1964. Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. Ecology 45:864–868.

Regalado, R. 1998. Approach distance and escape behavior of three species of Cuban *Anolis* (Squamata, Polychrotidae). Caribbean Journal of Science 34:211–217.

Revell L.J., M.A. Johnson, J.A. Schulte, II, J.J. Kolbe, and J.B. Losos. 2007. A phylogenetic test for adaptive convergence in rock-dwelling lizards. Evolution 61:2898–2912.

Ribeiro L.B., N.B. Silva, and E.M.X. Freire. 2012. Reproductive and fat body cycles of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata, Tropiduridae) in a Caatinga area of northeastern Brazil. Revista Chilena de Historia Natural 85:307–320.

Rocha, C.F.D., and H.G. Bergallo. 1990. Thermal biology and flight distance of *Tropidurus oreadicus* in an area of Amazonian Brazil. Ethology, Ecology and Evolution 2:263–268.

Rocha, W.J.S.F., J.M. Chaves, C.C. Rocha, L. Funch, and F.A. Juncá. 2005. Avaliação ecológica rápida da Chapada Diamantina. Pp. 29–45 *In* Biodiversidade e Conservação da Chapada Diamantina. Juncá F.A., L. Funch, and W.J.S.F. Rocha (Eds.). Ministério do Meio Ambiente, Brasília, Brasil.

Rodrigues, M.T. 1987. Sistemática, ecologia e zoogeografia dos *Tropidurus* do grupo *torquatus* ao sul do Rio Amazonas (Sauria, Iguanidae). Arquivos de Zoologia 31:105–230.

Rodrigues, M.T. 1988. Distribution of lizards of the genus *Tropidurus* in Brazil (Sauria, Iguanidae). Pp. 305–315 *In* Proceeding of a Workshop on Neotropical Distribution Patterns. Heyer, W.R., and P.E. Vanzolini (Eds). Academia Brasileira de Ciências, Rio de Janeiro, Brasil.

Smith, G.R., and J.A. Lemos–Espinal. 2005. Comparative escape behavior of four species of Mexican phrynosomatid lizards. Herpetologica 61:225–232.

Stiller, R.B., and L.D. McBrayer. 2013. The ontogeny of escape behavior, locomotor performance, and the hind limb in *Sceloporus woodi*. Zoology 116:175–181.

Vitt L.J. 1981. Lizard reproduction: habitat specificity and constraints on relative clutch mass. The American Naturalist 117:506–514.

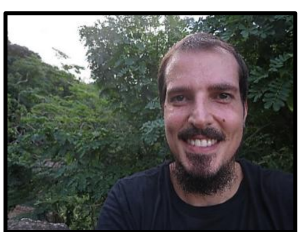
Vitt L.J. 1993. Ecology of isolated open-formation *Tropidurus* (Reptilia: Tropiduridae) in Amazonian lowland rain forest. Canadian Journal of Zoology 71:2370–2390.

Vitt L.J., and S.R. Goldberg. 1983. Reproductive ecology of two tropical iguanid lizards: *Tropidurus torquatus* and *Platynotus semitaeniatus*. Copeia 1983:131–141.

Vitt, L.J., J.P. Caldwell, P.A. Zani, and T.A. Titus. 1997. The role of habitat shift in the evolution of lizard morphology: evidence from tropical *Tropidurus*. Proceedings of the National Academy of Sciences of the United States of America 94:3828–3832.

Ydenberg, R.C., and L.M. Dill. 1986. The economics of fleeing from predators. Advances in the Study of Behavior 16:229–249.

Zar, J.H. 1999. Biostatistical Analysis. Prentice-Hall. Englewood Cliffs, New Jersey, USA.



THIAGO MAIA-CARNEIRO is a Ph.D. student in Ecology and Evolution at the Universidade do Estado do Rio de Janeiro (UERJ), with a dissertation about ecology and behavior of reptiles. He graduated with a Bachelor's in Biological Sciences at the UERJ, with a monograph on the ecology and behavior of amphibians, and he earned a M.Sc. in Ecology and Evolution at the UERJ with a thesis concerning ecology and behavior of reptiles. Thiago is studying the ecology of amphibians and reptiles in the Laboratório de ecologia de vertebrados at the UERJ. (Photographed by Thiago Maia-Carneiro).

CARLOS FREDERICO DUARTE ROCHA is a Professor of Ecology at the Departamento of Ecology, Institute of Biology at the Rio de Janeiro State University (UERJ) where he has worked since 1988. He received both his Master (1987) and Ph.D. (1992) degrees in Ecology from the Universidade Estadual de Campinas (UNICAMP) in Campinas, São Paulo State, Brazil. His main interests are in ecology and conservation of amphibians and reptiles. He has already supervised 29 Ph.D. students degree and 29 Master's students. He is an Adjunct Coordinator of the Graduate Program in Ecology and Evolution at UERJ and is the Leader of the Tropical Vertebrate Ecology Group of the Brazilian Council of Science and Tecnology (CNPq) of the Brazilian Environmental Ministry coordinating 101 researchers (44 Ph.D. researchers and 57 graduate and undergraduate students). (Photographed by Helena Godoy Bergallo).