Herpetological Conservation and Biology 9(1):48−56.
Submitted: 5 November 2012; Accepted: 26 August 2013; Published: 13 July 2014.

PATTERNS OF PREDATION AND ANTIPREDATOR BEHAVIOR IN THE AUSTRALIAN WATER DRAGON, *PHYSIGNATHUS LESUEURII*

J. SEAN DOODY[1], PETER HARLOW[2], DONNA DOUGLASS[3], JASON D. THIEM[4], BEN BROADHURST[5], DANE TREMBATH[6], JERRY OLSEN[7], ESTEBAN FUENTES[7], AND TONY ROSE[8]

[1]Department of Ecology and Evolutionary Biology, 569 Dabney Hall, University of Tennessee, Knoxville, Tennessee 37996-1610, USA, e-mail: jseandoody@gmail.com
[2]Taronga Zoo, PO Box 20, Bradleys Head Road, Mosman, New South Wales 2088, Australia
[3]Australian National Botanical Gardens, GPO Box 1777, Canberra, Australian Capital Territory 2601, Australia
[4]Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada
[5]Parks, Conservation, and Lands, ACT Department of Territory and Municipal Services, GPO BOX 158, Canberra, Australian Capital Territory 2601, Australia
[6]Museum and Art Gallery of the Northern Territory, GPO Box 4646, Darwin Northern Territory 0801, Australia
[7]Institute for Applied Ecology, University of Canberra, Australian Capital Territory 2601, Australia
[8]The Australian Museum, 6 College Street, Sydney, New South Wales 2010, Australia

***Abstract*.—Although lizards are more diverse in arid environments, many lizard taxa have independently invaded aquatic habitats. Adaptations in aquatic lizards are often straightforward (e.g., dorsolaterally compressed tails facilitate swimming), but what made these species invade aquatic habitats in the first place? Although this question is not directly testable, one possible reason is to reduce predation risk. Here we examine the fit of a species' antipredator behaviors to the predation risk associated with its known and suspected predators. We reviewed the literature for records of predation on the Australian Water Dragon, *Physignathus lesueurii*, a semi-aquatic lizard that uses aquatic escape and aquatic sleeping, but does not forage underwater. We then examined these two behaviors in relation to the patterns of predation revealed by our review. Our review identified 25 species of predators, most of which were aerial (mainly raptors) or terrestrial/arboreal (snakes, lizards, and mammals). Aquatic predators were rare. Our review supports the hypothesis that Water Dragons invaded and persist in aquatic habitats to decrease predation risk from terrestrial and aerial predators, although we cannot rule out the exploitation of an abundance of available (riparian) food as the primary reason for invading aquatic habitats. Future studies should test how well Water Dragons can thermoregulate by sleeping underwater (vs. in air), and could test the antipredator responses of Water Dragons to mock predators.**

Key Words.—**Agamidae; aquatic escape; aquatic lizards; aquatic sleeping; predation risk**

INTRODUCTION

Predator escape is an essential, adaptive behavior in animals, and researchers have devoted considerable thought and effort toward its evolution, context, correlates, and patterns (Ydenberg and Dill 1986; Lima and Dill 1990; Lima 1993; O'Steen et al. 2002; Cooper and Frederick 2007). One way to effectively escape predators is to rapidly change microhabitats (e.g., move to thicker cover; Lima and Dill 1990; Sih 1997; Cooper 1998). Even more effective is to rapidly move to where a predator cannot, or will not, follow (e.g., a mouse retreating into a small burrow when chased by a fox). Some semi-aquatic species use water bodies as escape microhabitat (e.g., frogs, mudskippers, snakes, crocodilians, ducks, and beavers), and there is evidence that their would-be predators often do not follow (Carpenter 1952; Gregory 1979).

Although lizard species richness is highest in arid regions (Pianka and Vitt 2003), some lizard species have invaded aquatic habitats. In a review, Bauer and Jackman (2008) revealed 73 lizard species from 11 families that regularly use aquatic habitats, noting the multiple, independent evolution of aquatic or semi-aquatic species. Use of the aquatic habitat includes diving, sleeping or foraging in or under water, or running over the water surface. Accordingly, many lizards have evolved adaptations for their aquatic existence, including morphological, physiological, and behavioral traits (Dawson et al. 1977; Courtice 1985; Hsieh and Lauder 2004; Schwenk 2008; but see Leal et al. 2002).

Adaptations in aquatic lizards are often straightforward; laterally compressed tails facilitate swimming, fringed toes aid in running over the water surface, and diving evades predators. However, it is often unclear why a particular species is aquatic; that is, what made the species invade the aquatic habitat in the first place? This question is more difficult to answer in species that both forage underwater and use aquatic escape because these species may have invaded the aquatic environment to access aquatic food, or to escape predators, or both.

A few lizard species that do not forage underwater use water as a refuge from predators, particularly when under immediate threat. For example, the Australian Water Dragon, *Physignathus lesueurii*, is seldom far from water, feeds terrestrially, and uses aquatic escape to reduce predation risk (Barrett 1931; Anonymous 1976; Retallick and Hero 1994). However, the water dragon also sleeps under water (Thompson 1993; Turner 1999; Meek and Avery 2008). Aquatic sleeping may also provide protection from terrestrial predators, but alternatively it may confer a thermal advantage because water temperatures are generally warmer than air temperatures at night (Turner 1999).

Which adaptation prompted the invasion of aquatic habitats in Water Dragons, the potential thermal advantage of aquatic sleeping, or predator avoidance via diving into water and/or aquatic sleeping? Although this question is not directly testable, we can determine the degree to which Water Dragons optimally exploit the aquatic medium by studying their thermoregulation (aquatic sleeping), or we can examine the fit of their behaviors (aquatic escape and aquatic sleeping) to predation risk associated with their known (extant) predators. Identifying actual and potential predators is critical to interpreting animal behavior (Lima and Dill 1990). Such information is often difficult to obtain for reptiles due to the paucity of direct observations of predation. However, the opportunity exists to determine the suite of predators by reviewing predation anecdotes and dietary studies of potential predators.

In this paper we address the predation risk hypothesis by reviewing the known predators of water dragons through examination of published dietary records of suspected predators (e.g., raptors) and by gleaning published and unpublished observations of predation events. We include detailed descriptions of predation events in a few cases to provide insights into predator avoidance and predator hunting tactics. We discuss how well the suite of identified and suspected predators matches the antipredator behaviors of Water Dragons, to address why they may have invaded their aquatic habitat.

MATERIALS AND METHODS

The Australian Water Dragon is a large, semi-aquatic agamid lizard inhabiting riparian zones along the eastern coast of Australia (Cogger 2000). Males approach 90 cm total length and 1.0 kg; females are up to 60 cm and 0.5 kg. The Water Dragon is omnivorous but predominantly carnivorous, feeding on insects and small vertebrates (Cogger 2000). It is generally heliothermic, basking on objects close to or above water, readily using aquatic escape when threatened (Cogger 2000), and can remain submerged for up to 90 min (Courtice 1985). Individuals can also take refuge up trees, in rock crevices, burrows, or caves (Sean Doody, pers. obs.). The Water Dragon sleeps submerged underwater, partially submerged, on vegetation overhanging the water, on rocks in water, in rock crevices, or in burrows or caves (Thompson 1993; Retallick and Hero 1994; Anthony and Telford 1996; Turner 1999).

We searched published journal articles, books, and book chapters, along with unpublished reports for evidence of predation on water dragons. These sources included dietary reviews and studies of known and suspected predators of Water Dragons (e.g., raptors, foxes, cats, and water rats), and anecdotal observations of predation. Anecdotes included published notes and unpublished observations from competent herpetologists or other biologists. We supplemented this information with four detailed accounts of predation events, and one ‘partial predation’ account on Water Dragons. We then reviewed the literature on the aquatic behavior of Water Dragons, examining the fit of these behaviors to the suite of predators we assembled. In this review we do not consider predation of Water Dragon eggs.

RESULTS

An exhaustive review of the literature revealed 25 known predators of Water Dragons (Table 1). The list was dominated by 11 species of birds, seven species of snakes, and three lizard species. Observations of predation by mammals (two species) and fish (two species) were rare. predominated; whereas, aquatic predators were rare (8%).

At about 1230 on 8 January 2007, we observed a 1.0–1.2-m long Eastern Brown Snake (*Pseudonaja textilis*) with an adult Water Dragon in its mouth, in the lower reaches of the Cotter River, Australian Capital Territory, Australia (35°20′45.94″S, 148°53′22.36″E). The snake was in the stream about 1 m from the bank and clinging to a small branch attached to the shore. The Water Dragon was up to its shoulders in the mouth of the snake and was kicking and lashing its tail. After a few minutes the snake detached from the branch and drifted downstream with the dragon, seeking purchase with its tail. We are unsure if the snake successfully swallowed the dragon. At 1025 on 24 December 2007, we observed a 1.3-m male Eastern Brown Snake with an adult female Water Dragon in its mouth at the Australian National Botanic Gardens (ANBG), Canberra, Australian Capital Territory, Australia (35°16′44.19″S, 149°06′37.74″E; Fig. 1). The snake held the dragon in its mouth for approximately 10 min after being discovered, and then dragged it under a rock ledge. The snake re-appeared and commenced swallowing the lizard head-first a few minutes later. Brown snakes have been observed chasing water dragons at the ANBG on seven other occasions, and one large male chased several water dragons continuously for 2.25 h. Similarly, an Eastern Brown Snake was found swallowing a juvenile Water Dragon at ANBG in October 2004 (Greg Sattler, pers. comm.). Elsewhere, we also observed an Eastern Brown Snake chase a juvenile Water Dragon down an

TABLE 1. Reported predators of the Australian Water Dragon (*Physignathus lesueurii*).

Predator	Common name	Reference
Reptiles		
Snakes		
Colubridae		
Boiga irregularis	Brown Tree Snake	Rettalick and Hero 1994
Dendrelaphis punctulatus	Common Tree Snake	Shine 1991
Elapidae		
Acanthophis antarcticus	Death Adder	Shine 1980; Hoser 1981*
Austrelaps superbus	Lowland Copperhead	Anonymous 1976
Pseudechis porphyriacus	Red-bellied Blacksnake	Anonymous 1976
Pseudonaja textilis	Eastern Brown Snake	Anonymous 1976**; Shine 1977; present study
Tropidechis carinatus	Rough-scaled Snake	Shine 1982
Lizards		
Agamidae		
Physignathus lesueurii	Water Dragon	Peter Harlow, pers. obs.
Varanidae		
Varanus varius	Lace Monitor	Weavers 1989+; Carter 1992, Hoser 1993**
Varanus rosenbergi	Rosenberg's Monitor	You Tube Video: http://www.youtube.com/watch?v=BDH23cv1ReU
Birds		
Accipitridae		
Accipiter fasciatus	Brown Goshawk	Rose 1973; Barker and Vestjens 1979; this study
Accipiter novaehollandiae	Grey Goshawk	Burton and Olsen 1997
Aquila audax	Wedge-tailed Eagle	Jerry Olsen et al., unpubl. data
Falco berigora	Brown Falcon	Jerry Olsen et al., unpubl. data
Haliaeetus leucogaster	White-bellied Sea Eagle	Olsen et al., 2006; Jerry Olsen et al., unpubl. data
Haliaeetus morphnoides	Little Eagle	Chris Barnes and Eric Zillmann, unpubl. data
Corvidae		
Corvus coronoides	Australian Raven	Sean Doody, pers. obs.***
Strigidae		
Ninox strenua	Powerful Owl	Kavanagh 2002++
Tyto novaehollandiae	Masked Owl	Kavanagh 2002++
Tyto tenebricosa	Sooty Owl	Kavanagh 2002++
Alcedinidae		
Dacelo novaeguineae	Laughing Kookaburra	Peter Harlow, pers. obs.
Mammals		
Felidae		
Felis catus	Feral Cat	Sean Doody, pers. obs+
Canidae		
Canis familiaris	Domestic Dog	Martin Whiting, pers. comm.
Fish		
Anguillidae		
Anguilla australis	Short-finned Eel	Peter Harlow, pers. obs.
Oncorhynchus mykiss	Rainbow Trout	Mark Lintermans et al. unpubl. data

* = snake died; ** = captive observation; *** = consumed tails only; + = killed but may not have been consumed; ++ = probably *P. lesueurii*.

embankment and into a creek, where the lizard dived to the bottom, but the snake did not follow.

On 3 March 2006 at approximately 1700, we noted a low-flying Brown Goshawk (*Accipiter fasciatus*) carrying, and then dropping, an adult female Water Dragon ca. 10 m from the water's edge at Blue Water Holes, New South Wales, Australia (35°37′21.57″S, 148°41′15.52″E). The lizard suffered an open wound at the right shoulder and moved slowly in circles suggesting the injury would prove to be fatal. The goshawk remained perched nearby while we examined the lizard, and may have reclaimed its prey after we abandoned it.

DISCUSSION

Our review of patterns of predation supports the hypothesis that Water Dragons invaded and persist in aquatic habitats to decrease predation risk from terrestrial and aerial predators, although we cannot rule out the possibility that they initially invaded aquatic habitats primarily to exploit an abundance of available (riparian) food. Competition is thought to drive niche partitioning (Gause, 1932), but the lack of dietary information for Water Dragons for comparison with heteropatric species precludes addressing this hypothesis. Aquatic predators were rare relative to terrestrial, arboreal, and aerial predators. Aquatic sleeping appears to be secondarily evolved; in some individuals and populations dragons sleep above water (Turner 1999).

According to our review, aquatic predators of Water Dragons are uncommon; only three aquatic species of animals preyed upon water dragons: the Short-finned Eel

FIGURE 1. Adult male Eastern Brown Snake (*Pseudonaja textilis*) holding captured adult female Australian Water Dragon (*Physignathus lesueurii*) in the Australian National Botanic Gardens in 2008. The paint on the snake was for individual identification in a separate study. (Photographed by Donna Douglass).

(*Anguilla australis*), the Rainbow Trout (*Oncorhynchus mykiss*), and the Water Dragon itself, and all of these involved juvenile dragons. Based on size and feeding strategy, aquatic predators of adult Water Dragons would be restricted to crocodiles (*Crocodylus porosus* and *C. johnstoni*), the Water Python (*Liasis mackloti*), Barramundi (*Lates calcarifer*), freshwater cod (*Maccullochella* spp.), and the Water Rat (*Hydromys chrysogaster*). Most of these species are tropical and would thus only overlap with Water Dragons in the far northern portion of the dragon's range (Cogger 2000). A dietary study of Murray Cod (*Maccullochella peelii*) and another large apex predator fish, the Golden Perch (*Macquaria ambigua*) failed to detect Water Dragons as prey (Ebner 2006). Unfortunately, dietary studies of Water Rats, Freshwater Crocodiles, and Saltwater Crocodiles were conducted outside the Water Dragon's range (Woollard et al. 1978; Taylor 1979; Webb et al. 1982). The Great-billed Heron (*Ardea sumatrana*), another tropical species, may be the only wetland bird capable of routinely ingesting an adult Water Dragon. There is little doubt that larger wetland birds that are generalist carnivores such as herons, egrets, cormorants, and darters would take juvenile Water Dragons. Similarly, the semi-aquatic Keelback Snake (*Tropidonophis maurii*) would only be a threat to juvenile Water Dragons due to the relatively small size of the former (Cogger 2000). Freshwater fish large enough to consume adult Water Dragons are generally rare within the water dragon's range. A Murray Cod consumed a large adult Water Skink, *Eulamprus heatwolei*, comparable in size to a sub-adult Water Dragon (David Rhind, pers. comm.), and a Rainbow Trout preyed upon a sub-adult Water Skink (*Eulamprus tympanum*) and a juvenile Tiger Snake (*Notechis scutatus*), both comparable in size to a hatchling or yearling Water Dragon (Lintermans 1992; Clear 2011).

In contrast, terrestrial predators of Water Dragons appear to be more common. Domestic Dogs (*Canis familiaris*), Feral Cats (*Felis catus*), six species of snakes and two species of lizards consume Water Dragons (Table 1). Domestic species may continue to select for antipredator behavior in Water Dragons, especially in urban and suburban areas. However, Water Dragons were absent from the dietary contents of cats from Canberra (Barratt 1997). Although not yet reported, other terrestrial species would doubtless prey on Water Dragons, including dingos, foxes, quolls, and several other species of snakes (including pythons). The Carpet Python (*Morelia spilota*) did not consume water dragons in captivity (Slip and Shine 1988). Dietary studies of some of these putative predators revealed no Water Dragons (e.g., Palmer 1995). However, dietary studies of terrestrial mammals may not have been conducted within the Water Dragon's range, and may have included individuals without access to rivers or streams (e.g., Bayley 1978; Catling 1988).

Aerial predators were the most commonly reported predators of Water Dragons, dominated by raptors (Table 1). All three eagles, three species of owls, two species of goshawks, and the Brown Falcon (*Falco berigora*) consume Water Dragons (Table 1). Although some of the Water Dragons reported in dietary samples may have been juveniles, the raptors are large enough to capture and kill adult Water Dragons, and this is supported by our observation above of the Brown Goshawk mortally wounding an adult female. Probable aerial predators include four other species of large owls, two species of kites, two species of harriers, and the Red Goshawk (*Erythrotriorchis radiatus*). The Laughing Kookaburra (*Dacelo novaeguineae*) is known to take juveniles (Table 1), which also likely fall prey to the Blue-winged Kookaburra (*D. leachii*) and two species of currawongs (*Strepara graculina* and *S. versicolor*).

A few probable, historical predators of Water Dragons are no longer a major threat. Aboriginal people still consume lizards in northern and western Australia, and although east coast tribes rarely hunt, they undoubtedly once did consume Water Dragons (aboriginals have names for Water Dragons, including 'Bajiri', Djirbal people south of Cairns; 'magil', Jagara people of the Brisbane area; 'Bidgawong', Darug people of the Sydney area). The Thylacine (*Thylacinus cynocephalus*) was a generalist predator formerly widespread in eastern Australia (van Dyck and Strahan 2008) that could have easily consumed Water Dragons.

Water Dragons possess one obvious antipredator behavior (aquatic escape) and another potential antipredator behavior (sleeping underwater), although the latter behavior may primarily reflect behavioral thermoregulation. When threatened, Water Dragons dive into the water, lie motionless on the bottom, and can remain submerged for up to 90 min (Courtice 1985).

Some individuals in some populations sleep submerged or partially submerged underwater (Turner 1999). Our review can provide insights into how predation risk shapes these two behaviors in Water Dragons but there are limitations. For example, we cannot ascertain if the predation records we collated involved sleeping dragons, although because Water Dragons are strictly diurnal, we can assume that predation by diurnal predators did not involve sleeping dragons. Our own observations of predation did not involve sleeping dragons. Although some of the known predators are mainly nocturnal (Rough-scaled Snake, *Tropidechis carinatus*; Brown Tree Snake, *Bioga irregularis*; three species of owls), the majority are diurnal, suggesting that most predation events did not involve sleeping dragons. Moreover, owls often take prey at dusk (Jerry Olsen, pers. obs.). Thus, we can hypothesize that predation risk in Water Dragons is highest during the day, when the species is active.

There are two obvious benefits to perching and foraging next to or above water. First, it would be more difficult for terrestrial predators to capture Water Dragons perched above water, compared to those on land. In many cases terrestrial animals would be precluded from reaching Water Dragons (e.g., on branches over water), except perhaps for arboreal animals, such as snakes. Second, once a dragon perched above water dives, its long submergence time (up to 1 h; Courtice 1985) probably ensures predator evasion against terrestrial and aerial predators. It is unlikely that a terrestrial, arboreal, or aerial predator would dive into the water and capture an escaping Water Dragon. This notion is supported by our observations of an Eastern Brown Snake giving up its chase on a juvenile water dragon that had dived to the bottom of a pool, and by observations of aquatic escape in frogs (Carpenter 1952; Gregory 1979). Although a terrestrially-perched dragon may find safety in a terrestrial refuge (e.g., thick cover, burrow); non-aquatic predator evasion might be less likely in that type of refugium compared to in water.

Aerial predation involving raptors preying upon lizards is widespread (Swanson 1950; Pianka and Vitt 2003). Although aquatic escape would be effective, raptors often ambush their prey by surprise, reducing the chances of (aquatic) escape. The majority of non-aerial predation of Water Dragons involved terrestrial predators. In this case, the water may not be simply a counterpart to a terrestrial cover, but rather may reflect a superior refuge from predation because although terrestrial predators would likely pursue their prey into terrestrial cover, few would follow Water Dragons into and under the water. Moreover, escaping to a burrow, crevice, tree hollow, or other refuge would generally be more difficult than diving into the water. The hunting tactics of the predator influence the probability of escape, and we hypothesize that aquatic escape is superior to 'terrestrial escape' when under attack by a terrestrial or aerial predator. An assumption of the 'superior aquatic refuge' hypothesis is that predation risk underwater is lower than predation risk above water. Our list of predators supports this assumption; aquatic predators were rare in our review compared to terrestrial and aerial predators.

Although Water Dragons use terrestrial sleeping sites (reviewed in Turner 1999), sleeping underwater may reduce predation risk to nocturnal, terrestrial predators. Alternatively, underwater sleeping may have been driven by a thermoregulation advantage because water temperatures are generally warmer than air temperatures during the night, especially in the cooler months (Turner 1999). Although water temperature averaged only 0.28° C warmer than air temperature when five water dragons sleeping under water were discovered on 19-28 February 1997 between 2034 and 2150 (Turner 1999), air temperatures would generally decline at a much faster rate, and to a greater extent, than water temperatures overnight. If underwater sleeping has an antipredator function, it may reflect the paucity of aquatic predators compared to terrestrial ones. Most records of Water Dragon predation did not involve sleeping dragons (nocturnal predators).

In summary, aquatic escape may have been the adaptive reason for the historical invasion of Water Dragons into the riparian zone, based on the terrestrial habitats of its nearest relatives and thus ancestor, and based on the apparent advantage of the behavior to an abundance of terrestrial and aerial predators. Water may be a superior escape habitat to a terrestrial refuge (burrows, trees, thick cover, or rock crevices) because of the relative ease of dropping directly and rapidly into the water. This behavior has also evolved independently in other semi-aquatic lizards and snakes (e.g., Cooper et al. 2008), making its future study within a comparative context warranted.

Acknowledgments.—We thank the following for providing predator-prey information: Chris Barnes, Stephen Debus, Esteban Fuentes, and Eric Zillmann. We thank Enzo Guarino, David Hunter, Will Osborne, Nadav Pezaro, and Mike Thompson for reviewing an earlier draft of the manuscript.

Literature Cited

Anonymous. 1976. Observations on the Eastern Water Dragon *Physignathus lesueurii* in the natural state and in captivity by A.H.S. members. Herpetofauna 8:20–22.

Anthony, M., and L. Telford. 1996. Observations of the Eastern Water Dragon (*Physignathus lesueurii*) in the northern wet tropics area, with a note on an unusual defensive behavior in a juvenile. Chondro 4:21–22.

Barker, R.D., and W.J.M. Vestjens. 1979. The Food of Australian Birds. CSIRO, Melbourne, Australia.

Barratt, D.G. 1997. Predation by House Cats, *Felis catus* (L.), in Canberra, Australia. I. Prey composition and preference. Wildlife Research 24:263–277.

Barrett, C. 1931. The Weekly Times Wild Nature Book. Herald and Weekly Times Ltd., Melbourne, Australia.

Bauer, A.M., and T. Jackman. 2008. Global diversity of lizards in freshwater (Reptilia: Lacertilia). Hydrobiologia 595:581–596.

Bayley, C.P. 1978. A comparison of the diets of the Red Fox and the Feral Cat in an arid environment. South Australian Naturalist 53:20–28.

Burton, A.M., and P. Olsen. 1997. Niche partitioning by two sympatric goshawks in the Australian wet tropics: Breeding-season diet. Wildlife Research 24:45–52.

Carpenter, C.C. 1952. Comparative ecology of the Common Garter Snake (*Thamnophis s. sirtalis*), the Ribbon Snake (*Thamnophis s. sauritus*), Butler's Garter snake (*Thamnophis butleri*) in mixed populations. Ecological Monographs 22:235–258.

Carter, D.B. 1992. Reproductive ecology of the Lace Monitor *Varanus varius* in southeastern Australia. Ph.D. Dissertation, Australian National University, Canberra, Australia. 158 p.

Catling, P.C. 1988. Similarities and contrasts in the diets of foxes, *Vulpes vulpes*, and cats, *Felis catus*, relative to fluctuating prey populations and drought. Australian Wildlife Research 15:307–317.

Clear, R.C. 2011. *Notechis scutatus* (Tiger Snake) predation. Herpetological Review 42:442.

Cogger, H. 2000. Reptiles and Amphibians of Australia. Reed New Holland, Sydney, Australia.

Cooper, W.E., Jr. 1998. Effects of refuge and conspicuousness on escape behavior by the Broad-headed Skink (*Eumeces laticeps*). Amphibia-Reptilia 19:103–108.

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

Cooper, W.E., Jr., O. Attum, and B. Kingsbury. 2008. Escape behaviors and flight initiation distance in the Common Water Snake *Nerodia sipedon*. Journal of Herpetology 42:493–500.

Courtice, G.P. 1985. Effects of hypoxia on cardiac vagal action in a lizard *Physignathus lesueurii*, and its contribution to diving bradycardia. Pp. 373–377 *In* Biology of Australasian Frogs and Reptiles. Grigg, G, R. Shine, and H. Ehmann (Eds.). Royal Zoological Society of New South Wales, Mosman, Australia.

Dawson, W.R., G.A. Bartholomew, and A.F. Bennett. 1977. A reappraisal of the aquatic specializations of the Galapagos Marine Iguana (*Amblyrhynchus cristatus*). Evolution 31:891–897.

Ebner, B. 2006. Murray Cod an apex predator in the Murray River, Australia. Ecology of Freshwater Fish 15:510–520.

Gause, G.F. 1932. Experimental studies on the struggle for existence. Journal of Experimental Biology 9:389–402.

Gregory, P.T. 1979. Predator avoidance behavior of the Red-legged Frog (*Rana aurora*). Herpetologica 35:175–184.

Hoser, R. 1981. Note on an unsuitable food item taken by a Death Adder (*Acanthophis antarcticus*). Herpetofauna 13:30–31.

Hoser, R. 1993. Notes on feeding interactions in Australian reptiles. Herpetofauna 23:32–35.

Hsieh, S.T., and G.V. Lauder. 2004. Running on water: three-dimensional force generation by basilisk lizards. Proceedings of the National Academy of Sciences 101:16784–16788.

Kavanagh, R.P. 2002. Comparative diets of the Powerful Owl (*Ninox strenua*), Sooty Owl (*Tyto tenebricosa*), and Masked Owl (*Tyto novaehollandiae*) in southeastern Australia. Pp. 175–191 *In* Ecology and Conservation of Owls. Newton, I., R. Kavanagh, J. Olsen, and I. Taylor (Eds.). CSIRO Publishing, Canberra, Australia.

Leal, M., A.K. Knox, and J.B. Losos. 2002. Lack of convergence in aquatic *Anolis* lizards. Evolution 56:785–791.

Lima, S.L. 1993. Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. Wilson Bulletin 105:1–47.

Lima, S.L., and L.M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Lintermans, M. 1992. Predation of *Eulamprus tympanum* by Rainbow Trout. Herpetofauna 22:34–35.

Meek, R., and R.A. Avery. 2008. Basking in the Australian Water Dragon *Physignathus lesueurii*; why do alpha males not respond to operative temperatures in the same way as adults and sub-adults? Amphibia-Reptilia 29:257–262.

Olsen, J., E. Fuentes, and J.B. Rose. 2006. Trophic relationships between neighboring White bellied Sea-eagles (*Haliaeetus luecogaster*) and Wedge-tailed Eagles (*Aquila audax*) breeding on rivers and dams near Canberra. Emu 106:193–201.

O'Steen, S., A.J. Cullum, and A.F. Bennett. 2002. Rapid evolution of escape ability in Trinidadian guppies (*Poecilia reticulata*). Evolution 56:776–784.

Palmer, R.A. 1995. Diet of the Red Fox (*Vulpes vulpes*) in south-western Queensland. Rangeland Journal 17:99–108.

Pianka, E.R., and L.J. Vitt. 2003. Lizards: Windows to the Evolution of Diversity. University of California Press, Berkeley, California, USA.

Rettalick, R.W.R., and J.M. Hero. 1994. Predation of an Eastern Water Dragon (*Physignathus leuserii*) by a common Brown Tree Snake (*Boiga irregularis*). Herpetofauna 24:47–48.

Rose, A.B. 1973. Food of some Australian birds. Emu 73:177–183.

Schwenk, K. 2008. Comparative anatomy and physiology of chemical senses in non-avian aquatic reptiles. Pp. 65–

81 *In* Sensory Evolution on the Threshold: Adaptations in Secondarily Aquatic Vertebrates. Thewissen, J.G.M., and S. Nummela (Eds.). University of California Press, Berkeley, California, USA.

Shine, R. 1977. Habitats, diets, and sympatry in snakes: a study from Australia. Canadian Journal of Zoology 55:1118–1128.

Shine, R. 1980. Ecology of the Australian Death Adder *Acanthophis antarcticus* (Elapidae): Evidence for convergence with the viperidae. Herpetologica 36:281–289.

Shine, R. 1982. Ecology of the Australian elapid snake *Tropidechis carinatus*. Journal of Herpetology 16:83–387.

Shine, R. 1991. Constraints, allometry, and adaptation: food habits and reproductive biology of Australian Brown Snakes (*Pseudonaja*: Elapidae). Herpetologica 45:195–207.

Sih, A. 1997. To hide or not to hide? Refuge use in a fluctuating environment. Trends in Ecology and Evolution 12:375–376.

Slip, D.J., and R. Shine. 1988. Feeding habits of the Diamond Python, *Morelia s. spilota*: ambush predation by a boid snake. Journal of Herpetology 22:323–330.

Swanson, P.L. 1950. The Iguana *Iguana iguana iguana* (L). Herpetologica 6:187–193.

Taylor, J.A. 1979. The food and feeding habits of subadult *Crocodylus porosus* Schneider in northern Australia. Australian Wildlife Research 6:347–359.

Thompson, M.B. 1993. Estimate of the population structure of the Eastern Water Dragon, *Physignathus lesueurii* (Reptilia: Agamidae) along riverside habitat. Wildlife Research 20:613–619.

Turner, G. 1999. Field observations of Gippsland Water Dragons *Physignathus lesueurii howitti* sleeping in water. Herpetofauna 29:49–51.

Van Dyck, S., and R. Strahan. 2008. The Mammals of Australia. 3rd Edition. Reed New Holland, Sydney, Australia.

Weavers, B.W. 1989. Diet of the Lace Monitor *Varanus varius* in southeastern Australia. Australian Zoologist 25:83–85.

Webb, G.J.W., S.C. Manolis, and R. Buckworth. 1982. *Crocodylus johnstoni* in the McKinlay River Area, N.T. I. Variation in the diet, and a new method of assessing the relative importance of prey. Australian Journal of Zoology 30:877–899.

Woollard, P., W.J.M. Vestjens, and L. Maclean. 1978. The ecology of the Eastern Water Rat *Hydromys chrysogaster* at Griffith, NSW: food and feeding habits. Australian Wildlife Research 5:59–73.

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

SEAN DOODY is an Adjunct Researcher at the University of Tennessee (USA) and the University of Newcastle (Australia). He received his B.S. from Louisiana State University, his M.S. from Southeastern Louisiana University, and his Ph.D. from the University of Canberra (Australia). His current research projects include climate warming responses in animals with environmental sex determination, social behaviour in reptiles, communal nesting in reptiles and amphibians, impacts of invasive cane toads on native animals, conservation of threatened reptile species, embryo ecology in reptiles, and predator-prey relationships between crocodiles and wallabies. (Photographed by Michael Anthony).

PETER HARLOW is the Manager of the Herpetofauna Division at Taronga Zoo, Sydney, Australia, and is currently involved in conservation programs for the Fijian Crested Iguana (*Brachylophus vitiensis*), two Critically Endangered Australian lizard species from Christmas Island, and six Critically Endangered Australian frog species. Over his three decade-long career he has worked on ecology and conservation biology projects on a wide variety of reptile and amphibian species, mostly in Australia but also working in Southern Africa, Indonesia, USA, Canada, and Fiji. (Photographed by Joe Wasilewski).

JASON THIEM is a Ph.D. student with the Fish Ecology and Conservation Physiology Laboratory at Carleton University (Ottawa, Canada). He received his B.S. (Hons) from the University of Canberra (Australia). His thesis focuses on the effects of dams on sturgeon migration and reproductive behaviour, as well as the biomechanics and energetics of sturgeon passage through fishways. (Photographed by Keith Stamplecoskie).

DONNA DOUGLASS is currently employed by the Department of Defence, having completed a B.Sc. with the University of New South Wales, Graduate Diploma from RMIT University, and her Master's in Applied Science (Environmental Conservation) at Charles Sturt University. Her primary area of interest is the conservation of reptiles, particularly venomous snakes. (Unknown Photographer).

BEN BROADHURST is an Aquatic Ecologist at the Institute for Applied Ecology at the University of Canberra, Australia. He received his B.Sc. from the University of Canberra. His primary research interests are spatial ecology of freshwater fish, conservation biology of Threatened fish species and assessment of Threatened fish populations. His current projects include assessment of the impacts of reservoir enlargement on threatened fish species and research into natural barriers to migration of Macquarie Perch (*Macquaria australasica*). (Photgraphed by Tim Kaminskas).

DANE TREMBATH is a Senior Zoological Consultant at EcOz Environmental Services and longtime Research Associate of the Museum and Art Gallery of the Northern Territory, Australia. Having had a lifelong love of reptiles, he completed his B.Sc. at James Cook University, Townsville, North Queensland and also a Master's on the Ecology of Krefft's River Turtle in the Townsville area. His primary research focus is on the ecology and taxonomy of snakes and turtles inhabiting tropical Northern Australia. (Photographed by Kathryn Dwyer).

JERRY OLSEN received his B.A. in Education at Washington State University in 1972 and his B.Sc. in Psychology and Zoology at Australian National University 1977. He received a Master's in Education at the University of Canberra in 1983 and a M.S. in Ecosystems Management at the University of New England in 1989. Jerry has studied birds of prey in the Canberra, Australia region since 1975 and published some 100 papers and articles and five books on raptors. In 2002, with Susan Trost, Michael Wink, and Hedi Sauer-Gürth, he discovered and named a new species in Indonesia, the Little Sumba Hawk-owl, *Ninox sumbaensis*. In 2005 he alerted researchers to the catastrophic decline in Little Eagle (*Hieraaetus morphnoides*) in the Australian Capital Territory and has since worked with ACT Parks and Conservation and the Canberra Ornithologists Group to document this decline and explain it. In 2012, his book *Australian High Country Owls*, received a Whitley Award. (Photographed by Susan Trost).

ESTEBAN FUENTES received his B.S. from UDLA in 2001, where he got *magna cum laude* for his Honours research on the human impact of the behaviour of captive felids. He received his M.S. at the University of Canberra in 2006, since then he is studying the ecology of birds of prey in the Canberra region (Australia), with special interest on their foraging patterns, guild interactions and the impact of urbanization in this group. His work also covers research on Wedge-tailed Eagle's *Aquila audax* behaviour and predator-prey relationships with Macropods. His research interests include captive welfare of wild animals, re-introduction programs and mathematical models in ecology. He currently lives in Mexico. (Picture by Jerry Olsen)

ANTHONY 'A.B.' ROSE is a keen naturalist and has been an associate of the Australian Museum for many years. Tony is an expert at analyzing raptor pellets, picking apart each casting to determine what the owls have eaten. Tony, a retired dairy farmer living in Forster, New South Wales, Australia, has conducted many studies and published widely. He is self-taught, has a prodigious knowledge of natural history and the capacity for hours of detailed work on Boobook prey. Tony has a private collection of insects, spiders, birds, mammals, and reptiles to crosscheck against the pieces of animals that other researchers find. He can identify mammal hairs, bird beaks, legs, feathers, and spider mouthparts of the animals that owls prey upon, and from these, he can robustly estimate the minimum number of prey. (Photographed by Jerry Olsen).