

ETHOGRAM OF *ABDOPUS ACULEATUS* (D'ORBIGNY, 1834) (CEPHALOPODA: OCTOPODIDAE): CAN BEHAVIOURAL CHARACTERS INFORM OCTOPODID TAXONOMY AND SYSTEMATICS?

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(Received 5 August 2006; accepted 22 February 2007)

ABSTRACT

An ethogram is provided for the small, intertidal, diurnal octopus *Abdopus aculeatus* (d'Orbigny, 1834). Information is based primarily on *in situ* observations of adults, and supplemented with photographs of animals in aquaria. Aspects of the dynamic display, mating system, activity patterns, and habitat use appear similar to those expressed by other members of *Abdopus*, as well as the large sister taxon *Octopus cyanea*, suggesting that these behaviours may be conserved throughout the evolution of these octopuses. Many skin components are also shared with *Octopus bimaculoides*, which may reflect either an evolutionary affinity with this octopus, or convergence in these characters. If behavioural units such as those documented here are compiled in a consistent manner for other species, then they may facilitate taxonomic identification, as well as future evolutionary studies of octopodids.

INTRODUCTION

Abdopus aculeatus (d'Orbigny, 1834) is an intertidal octopus described from the Philippines and common throughout Indonesia and northeastern Australia (Norman, 1993; Norman & Sweeney, 1997; Norman & Finn, 2001). Although this small species demonstrates among the most complex crypsis of any octopus (Norman & Finn, 2001), individuals can be remarkably easy to locate and follow in the wild. They are found in moderate densities, their tropical intertidal habitat is accessible to snorkelers, and they are large enough to be observed easily from a distance. These characteristics allow for extended behavioural observations without the disturbance or logistical limits imposed by the need to use dive lights, SCUBA or boats.

This paper presents ethological and natural history information obtained during an extensive behavioural study of *A. aculeatus* in the wild (Huffard, 2005). Observation taken during a study of locomotion in a large semi-natural aquarium (Huffard, 2006) supplemented these field observations. This ethogram expands on preliminary notes, illustrations and photographs provided for this species in Norman & Sweeney, (1997), Norman & Finn (2001) and Huffard (2006). The primary focus covers behaviours [defined as 'movement(s) (or lack of movement- e.g., in "freezing" in response to a predator) of the organism as a whole or any of its external parts' (de Queiroz & Wimberger, 1993)], including the tangible products of behaviour such as prey middens or a constructed den. Ecological characteristics such as prey items, substrate type and habitat use are included because they might reflect the octopus's movements toward a preferred area.

Octopodids can change their visual appearance rapidly and with great flexibility, an ability that is constrained by skin anatomy (Packard & Hochberg, 1977). The complexity and number of skin components, pigment composition of chromatophores and muscle structure within the skin vary considerably between each type of octopus, creating species-specific

repertoires of body patterns and skin textures (Packard & Hochberg, 1977; Hanlon, 1988; Messenger, 2001). Body patterns and aspects of skin anatomy (papillae, texture, white components and dark components) are presented here for *A. aculeatus*, and discussed as they relate to resting camouflage, displays and other behavioural expressions.

MATERIAL AND METHODS

A total of 167 animals were observed in the wild [North Sulawesi, Indonesia (1°35.94'N, 124°46.89'E) and Southeast Sulawesi (5°27.72'S, 123.68'E); 2000–2003] for approximately 790 observation hours, including 388 h during which animals were active at or away from their dens. Focal animal surveys (Altmann, 1974; Mather, 1991a; Forsythe & Hanlon, 1997; Hanlon, Forsythe & Joneschild, 1999) were conducted by following one or more individuals for as long as possible (up to 13 h including periods of confirmed inactivity), while recording activity in written code on underwater paper. Frames were obtained from video recorded on mini-DV with a Sony DCR-VX-2000 in an Amphibico underwater housing with ambient light. Unless stated otherwise, information presented is based on *in situ* observations of adults.

Additional observations were made of animals in Cape Tribulation, Queensland, Australia (16°4.15'S, 145°28.1'E; five animals in the wild, approximately 7 h of direct observation in 2003) and Lizard Island, Queensland, Australia (14°40'S, 145°28'E; a total of 18 animals observed briefly *in situ*, collected from the wild and housed in aquaria, in 2003 and 2005). Animals from Lizard Island were photographed in aquaria (CLH – Sony Cybershot W-7 with Sony Marine Pack in ambient light, taken in 2.5 m diameter semi-natural tank with flow-through seawater; Roy L. Caldwell – Nikon N90s with Micro Nikkor 105 macro lenses, and Nikon 200 camera, both with twin Nikon SB-800 strobes, taken in approximately 20-l recirculating tank with pebble and live-rock substrate).

Habitat use and predator–prey interactions were recorded. Habitat was characterized by noting the substrate in areas foraged and at the location of den. The locations of octopus dens mapped in five 10 × 20 m plots were compared to a

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Poisson distribution to determine if they were clumped, spaced evenly, or distributed randomly in these areas. Clumped distributions yield a coefficient of dispersion greater than one (see Ripley, 1981, for methods). Because individuals can move into each other's dens (Forsythe & Hanlon, 1997), the duration of den occupancy was estimated based on casual long-term observations of individuals that were identifiable by arm injury (as with *O. cyanea* and *O. briareus* in Yarnall, 1969, and Aronson, 1989, respectively). Temperatures in North Sulawesi were recorded using two StowAway® TidbiT® temperature loggers placed into former octopus dens from May to August 2001. A hand-held refractometer was used to determine salinity of water pipetted from octopus dens at low tide.

Thirty octopuses were caught with a dip net at the end of a foraging bout to identify food items carried in the web. Because drill holes can be very small (Dodge & Scheel, 1999), bivalve shells and remains of stomatopod crustacean prey were examined for drill holes and bite marks using a microscope with a light source. Fish were identified if they elicited a response from octopuses either at their dens or while foraging. Prey items, fish and algae in the area were identified to the lowest possible taxon according to Cribb (1996), Allen (1997) and Matsuura, Sumadhiharga & Tsukamoto (2000).

Terminology used for skin 'components' and behaviours follow those defined and illustrated by Packard & Sanders (1971), Packard & Hochberg (1977), Hanlon & Hixon (1980), Forsythe & Hanlon (1988), Hanlon (1988), Hanlon & Wolterding (1989), Cigliano (1993), Forsythe & Hanlon (1997), Norman & Sweeney (1997) and Norman (2000). The greenish iridescent sheen refers to that produced by a reflective layer of iridocytes in the skin, described in Hoyle (1885) and Packard & Hochberg (1977).

RESULTS: ETHOGRAM OF *ABDOPUS ACULEATUS* (D'ORBIGNY, 1834)

Behaviours and body patterns are summarized in Table 1 and Figures 1 and 2.

Habitat characteristics of Abdopus aculeatus

Abdopus aculeatus occupied dens in sandy bench on intertidal reef flats. Individuals clumped in small-scale plots (average coefficient of dispersion = 1.2), as well as along a beach (1,500 m²) (C. Huffard, G. Ashton & C. Biggens, unpubl.). Middens were rarely seen at the entrance of dens. Rather, den entrances were surrounded by pebbles (typically 1–5 cm diameter). Dens of large females in dens 'adjacent' to males were typically surrounded by a pile of at least 20–50 pebbles ('adjacent' defined here as being sufficiently close that the male could extend his hectocotylus to the female's den while sitting at his own). Dens of males and smaller individuals typically had fewer (typically 10 or fewer) pebbles at the entrance. Prominent algae and seagrasses in the area included *Cymodocea serrulata*, *Halophila ovalis*, *Halodule pinifolia*, *Laurencia papillosa*, *Padina australis* and *Thalassia hemprichii*. *Sargassum* sp. was found in their habitat only on Cape Tribulation, Australia. *Abdopus aculeatus* were not found living or foraging in close association with live coral on Sulawesi, but they did live near and forage among it in Queensland, Australia. Although a few individuals visited a secondary den while feeding and resting throughout the day, casual monitoring of holes showed that *A. aculeatus* typically spent the night in the same primary den for up to two weeks and perhaps longer. Juveniles were also intertidal. They were observed occupying large pieces of rubble, holes in sandy bench, and/or burrows in deep sand, often within a few metres of the mean low tide line.

Water temperatures in former dens in North Sulawesi ranged from less than 27°C at high tide to more than 37°C during mid-day low tides in the summer. Salinity at low tide ranged from approximately 22–40 ppt during the rainy and dry seasons, respectively.

Activity

Abdopus aculeatus became active at their dens at approximately sunrise. Qualitatively, most foraging occurred between mid-falling, low and mid-rising tides. Mating occurred throughout the day but was most common in the morning and afternoon. In Sulawesi, individuals returned to their dens before the lowest point of the tides while this appeared to be the peak of activity in Queensland. In the late afternoon they tended to their dens by pulling pebbles and small rubble close to the entrance. In Sulawesi *A. aculeatus* typically entered dens between 1,530–1,830 h, pulling pebbles over the entrance. Although Norman & Finn (2001) report occasionally seeing *A. aculeatus* out at night, no nocturnal activity was observed of *A. aculeatus* in North Sulawesi during two full nights of watching the entrances of two individuals remotely with an infrared video camera, and approximately 20 h of night-snorkels.

General body patterns

Octopuses spent most of their time expressing mottled ochre, gray or browns (Figs 1A–C, G, I–N, 2A, E) that resembled their habitat. Individuals in bright light also reflected a green iridescent sheen (Fig. 1B, F). These forms of resting camouflage involved less intense expression of papillae compared to that used during acute camouflage given in the presence of a potential predator (Fig. 1I). The body pattern of brown with a pale medial stripe (Fig. 1E, H) was performed almost exclusively by *A. aculeatus* near large amounts of seagrass. When giving this pattern the mantle was typically upright, the body elongate and the octopus drifted or crawled along with the surge. When the lateral neck dark spots (Fig. 1B, M) were visible while mantle hung down behind the head they gave the appearance of dark false eyespots.

The display of pale background with dark longitudinal stripes ('BWS') was performed most often by males in the presence of a female (Fig. 2B, C). Females were also capable of showing it, although this was not common (Fig. 2D). When expressed by guarding males this display also often involved a digitate papilla raised above each eye. As with other displays, octopuses were capable of showing 'BWS' on only one side of the body (Fig. 2C).

Skin texture was comprised of a faint 'patch and groove' system, which was difficult to discern among the well-developed system of secondary papillae.

Foraging and predatory behaviour

Abdopus aculeatus foraged via tactile means ('groping' and 'pouncing' on rocks and clumps of algae, digging into deep sand for crabs). They also foraged visually for portunid and calappid crabs, sometimes crawling or swimming approximately 3–5 m to catch one. The diet was largely crustacean, although two bivalves and two gastropods were consumed. Prey preference studies were not performed. No drill holes were found in molluscan or stomatopod prey. Crustaceans other than stomatopods were not examined for drill holes. On occasions when prey items were consumed at the den, *A. aculeatus* sometimes carried the empty exoskeletons up to 1 m from the den entrance to discard them. Currents then quickly removed most middens, leaving only heavier items such as *Calappa* exoskeletons.

BEHAVIOUR OF *ABDOPUS ACULEATUS*
Table 1. Checklist of behavioural characters for *Abdopus aculeatus*.

Functional group	Behavioural Unit	Character states
Habitat characteristics	General habitat	Reef flat, seagrass, sandy bench
	Depth	Intertidal
	Energy level	Areas with strong periodic tidal currents
	Den microhabitat	Reef flat tidepool or reef-flat shallows
	Den occupancy	Days, weeks
	Gather objects to den entrance	Yes (pebbles typically 1–5 cm diameter)
	Small scale density:	Maximum recorded: 10 adults/200 m ² (18 total individuals/200 m ²)
	Aggregation	Occurs
Activity	Operational sex ratio	1.8 males:1 female of reproductive size
	Circadian rhythms	Diurnal
	Peak hours of:	Mating: throughout the day Foraging: throughout the day Den-construction/excavation: morning, late afternoon
General body patterns	Tidal preference	Sulawesi: mid-tides (falling, rising); Queensland: low
	Resting behaviour	Sit atop den entrance with eyes erect and arm crown exposed
General body patterns	Components	<i>Distinct fixed white components:</i> dorsal mantle white spots, frontal white spots, arm spots, head white spot, transverse mantle bar, medial neck white spot. <i>Distinct fixed dark components:</i> star-like pattern around eye, lateral neck dark spots, dark arm bars, dark sucker rims observed in large males; dark longitudinal stripes adjacent to pale stripes down arm crown, extends down ventro-lateral edge of arms I. <i>Other components:</i> two thin longitudinal yellow lines down frontal arm crown; pale medial stripe down mantle and arm crown. <i>Ocelli:</i> not present
	Skin sculpture and papillae	<i>Primary papillae</i> in diamond configuration on dorsal mantle, with smaller secondary papillae scattered over the dorsal and ventral mantle, arm crown, and down arms; supraocular papillae present, elongate; two sub-ocular papillae small, flap-like (Fig. 1 N). Posterior mantle papilla flap-like, lobate, or branched (Fig. 1C, E, G, J, K, N). <i>Papillae shape:</i> unbranched digitate (seen only in supraocular papillae during expression of 'BWS'), lobate, flap-like (Fig. 1C), pointed with primary branching (Fig. 1D, E, G). Papillae expression extensive during acute camouflage (Fig. 4C); <i>Skin sculpture:</i> fine patch and groove system
	Body patterns	Variable (Figs 1, 2). <i>Consistent patterns include:</i> (1) ochre or grey resting camouflage with dorsal mantle white spots, transverse mantle bar, arm white spots, frontal white spots, head white spot, primary papillae branched or flap-like, secondary papillae branched or conical, and sometimes lateral neck dark spot, medial neck white spot, occasionally with dark longitudinal stripe adjacent to pale longitudinal stripe; (2) dark brown with pale medial stripe and limited expression of papillae; (3) conical mantle, pale mantle and arm crown, dorsal mantle white spots, thin ochre stripes down arm crown, arms brown with prominent white spots and pale patches nearly producing bars, papillae expression minimal, shaggy, except for prominent, lobate posterior mantle papilla; (4) Dark brown body with prominent white patches and spots; (5) Pale background with dark longitudinal stripes ('BWS'); Passing cloud observed. <i>Dymantic display:</i> dark background with white spots over the mantle, arm crown and arms; dark eye bar most visible in this display. <i>Iridescence:</i> green iridescent sheen visible on all surfaces (especially base of funnel underneath mantle) in bright ambient light
Foraging behaviour	Substrate foraged	Seagrass, algae, sandy bench and rubble of reef flat, deeper sandy areas between rocks and bench on reef flat, tidepool (crawl out of water: no)
	General means of detecting prey	Tactile ('groping' and 'pouncing'), visual
	Mode	Foraging bouts away from the den; lie-in-wait opportunist for portunid and calappid crabs
	Means of opening prey	Drill holes: not observed in bivalves (shell width approximately 10–15 mm); bite marks: observed in membranes between carapace and first thoracic somite in stomatopods; pry open: small bivalves; break open: crustaceans
	Prey captured <i>in situ</i>	Crustacea (common prey items): <i>Calappa hepatica</i> , <i>Gammarus</i> spp., <i>Gonodactylus chiragra</i> , <i>Gonodactylus viridis</i> , <i>Menaethius monoceros</i> , <i>Pagarus</i> spp., <i>Panaeus</i> spp., <i>Pilumnus verspertillo</i> , <i>Portunus granulatus</i> , <i>Xanthidae</i> Mollusca (one each): <i>Tellina</i> , <i>Strombus gibberulus</i> , <i>Cypraea helvola</i> , small unidentified bivalve
Defence	Prey preference	Not measured
	Ink, when released from animal:	Diffuse (North Sulawesi) and maintained integrity in water column for minutes (Southeast Sulawesi; Queensland, Australia)
	Ink colour	Brown
	Other reaction to threat	Remain still; flatten to substrate or lower into hole; jet; 'punch' with one or two curled arms (arms I) or 'whip' with one or two straight arms (one arm I, both arms I, or two adjacent arms I and II); arm autotomy

Continued

Table 1. Continued

Functional group	Behavioural Unit	Character states	
Agonistic interactions	Alarm reaction	Dymantic display (Fig. 1D): dark background with white spots of varying sizes on the mantle, arm crown and arms; dark eye bar visible; body flares, spreading arms and web	
	Burying behaviour	Juveniles; not observed in adults	
	Aggressive interactions	Observed in mate guarding situations	
	Types of agonistic interaction	Display [dark longitudinal stripes over a pale background ('BWS'); flamboyant display (Fig. 1K)]. Stand erect; approach/retreat from conspecifics; arms touch; whip with straight arm; grapple. Cannibalism observed <i>in situ</i> . yes (one case: whole animal, one case: two arms); 'Sucker display' (Packard, 1961), 'ligula display (Voight, 1991 b)' and 'fighting display' (Packard & Sanders, 1971) not observed	
Mating behaviour	Copulation approach	Distance only. 'mount' position not observed	
	Copulation duration	Seconds, minutes (maximum approximately 30 min)	
	Copulation location	At den; away from den while foraging	
	Mate guarding	Occurs	
	Sneaker mating	Occurs (using visual segregation from guarding male, either by hiding behind rocks or using slow movements and acute camouflage)	
Brooding	Displays	<i>Male typical</i> : dark and pale longitudinal stripes as during aggression <i>Female typical</i> : dorsal arms I raised and curled at tips ('DACT') <i>Both</i> : 'mantle bounce display' Stand tall at a den in presence of individual of opposite sex, exhibit dark and pale longitudinal stripes, raise and lower mantle every 3 s	
	Adjacent dens	Present	
	Migration to mating grounds	Not observed	
	Location	Unconfirmed, presumed in den in sandy bench (last known location of females before presumed brooding period)	
	Egg placement	Attached eggs in festoons (festoons < approximately 3 cm unbranched, longer festoons sometimes branched)	
	Timing of egg-deposition	All eggs probably laid within one week	
	Life history	Semelparous	
	Hatchling behaviour	Planktonic	
	Locomotion	Benthic	<i>Crawling</i> : mantle upright with or without tightly coiled arms; mantle hanging down behind head with arms sprawled around the body; mantle and arms form a compact ball; <i>Bipedal walking and Multi-armed walking</i> : arms coiled and raised above the body, or held close to the body, walking always on arm pair IV
		Swim above substrate	<i>Jet (backward swimming)</i> : body elongate, skin smooth; elongate with arm tips curled; <i>Medusoid backward swimming</i> ; <i>Forward swimming</i> : ranged from head raised and arms trailing below the body to head and body dorso-ventrally compressed with arms held to the side of the body, skin smooth

Defence

Camouflage was the primary defence of *A. aculeatus* although the degree of crypsis was not measured.

Octopuses reacted to or interacted with the following fish while foraging or at the den in Sulawesi: cigar wrasse (*Chelio inermis*), starry moray (*Echidna nebulosa*), bluefin trevaly (*Caranx melampygus*), giant trevaly (*Caranx ignobilis*), wrasses (*Stethojulis* spp.), thumbprint emperor (*Lethrinus harak*), black-spot triggerfish (*Rhinocanthus verrucosus*), crescent grunter (*Terapon jarbua*), cf. scissor-tail sergeant major (*Abudufduf* cf. *sexfasciatus*) cf. onespot demoiselle (*Chrysiptera* cf. *unimaculata*), flowery flounder (*Bothus mancus*), forktail rabbitfish (*Siganus argenteus*), cf. spotted rabbitfish (*Siganus canaliculatus*) and drummer (*Kyphosus* sp.). A number of

other predatory fish [including black tip reef sharks (*Carcharhinus melanopterus*), blue-spotted rays (*Taeniura lymma*), spiny devilfish (*Inimicus didactylus*) and estuarine stonefish (*Synanceia horrida*)] were seen within metres of the octopus' dens, but were not observed interacting with or eliciting reactions from the individuals. No act of predation was observed, but larger black-spot triggerfish, thumbprint emperorfish, and cf. scissor-tail sergeant major picked up octopuses by an arm and shook them, or pecked strongly at their heads and arms. Damsel fish repeatedly swam quickly toward them and pecked their head and arms, while cigar wrasses pecked at the arms and consumed dropped prey items.

The octopuses responded to fish by (1) ceasing movement (including ventilation); (2) flattening to the substrate or lowering into the den; (3) increasing the degree of crypsis by raising

mantle bar (3); photograph by R. Caldwell. **D.** Dymantic display of flared web dark background with white spots all over body, and dark eye bar (4). **E.** Upright crawling dark with pale medial stripe (5). **F.** Ochre resting camouflage with faint green iridescence (6) and adjacent pale and dark longitudinal arm crown stripes (7); photograph by R. Caldwell. **G.** Close-up of mantle and arm crown with star-like pattern of bars around the eye (8), and dark longitudinal stripe that extends down the arm crown and arms; photograph by R. Caldwell. **H.** Upright crawling with dark background and pale medial stripe, and tightly coiled arms. **I.** Acute camouflage. **J.** Crawling with conical mantle, arm bars, arm white spots and two ochre stripes down dorsal arm crown (9). **K.** Flamboyant display; note helically coiled arms, white transverse mantle bar and arm crown stripes. **L.** Pale mottled resting camouflage with dark arm bars and arm white spots (10). **M.** Grey resting camouflage with medial neck white spot (11) and lateral neck dark spots (12); photograph by R. Caldwell. **N.** Ochre resting camouflage with laterally branched primary papillae (13) and dorsal mantle white spots (14).

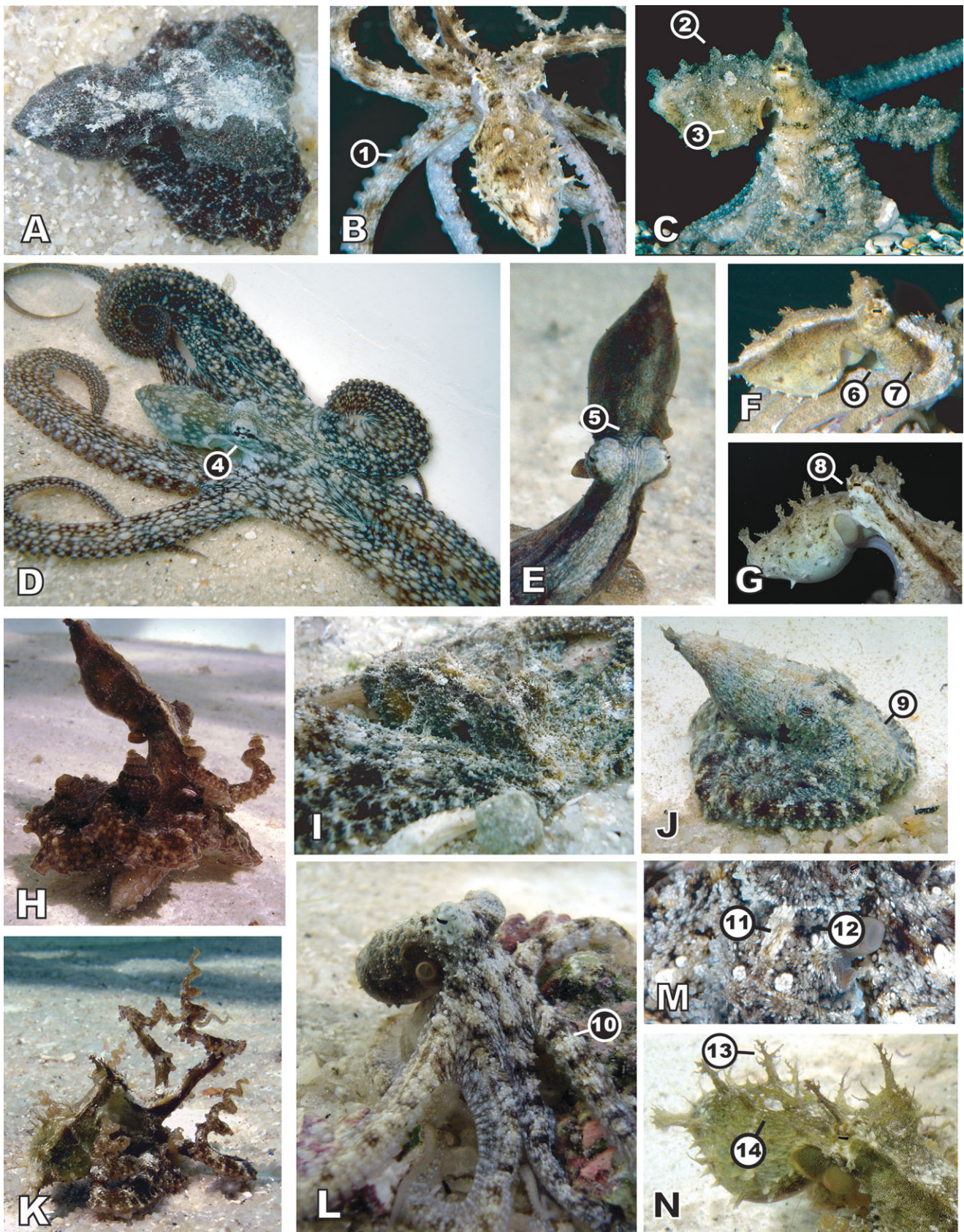


Figure 1. Chromatic and papillary skin components and postures of *Abdopus aculeatus*. **A.** Dark resting camouflage with white branched papillae on dorsal mantle and arm crown. **B.** Ochre-mottled resting camouflage with lateral neck dark spots, medial neck white spot, green iridescence and dark arm bars (1); photograph by R. Caldwell. **C.** Ochre-mottled resting camouflage, with flap-like unbranched primary papillae (2) and white transverse mantle bar (3);

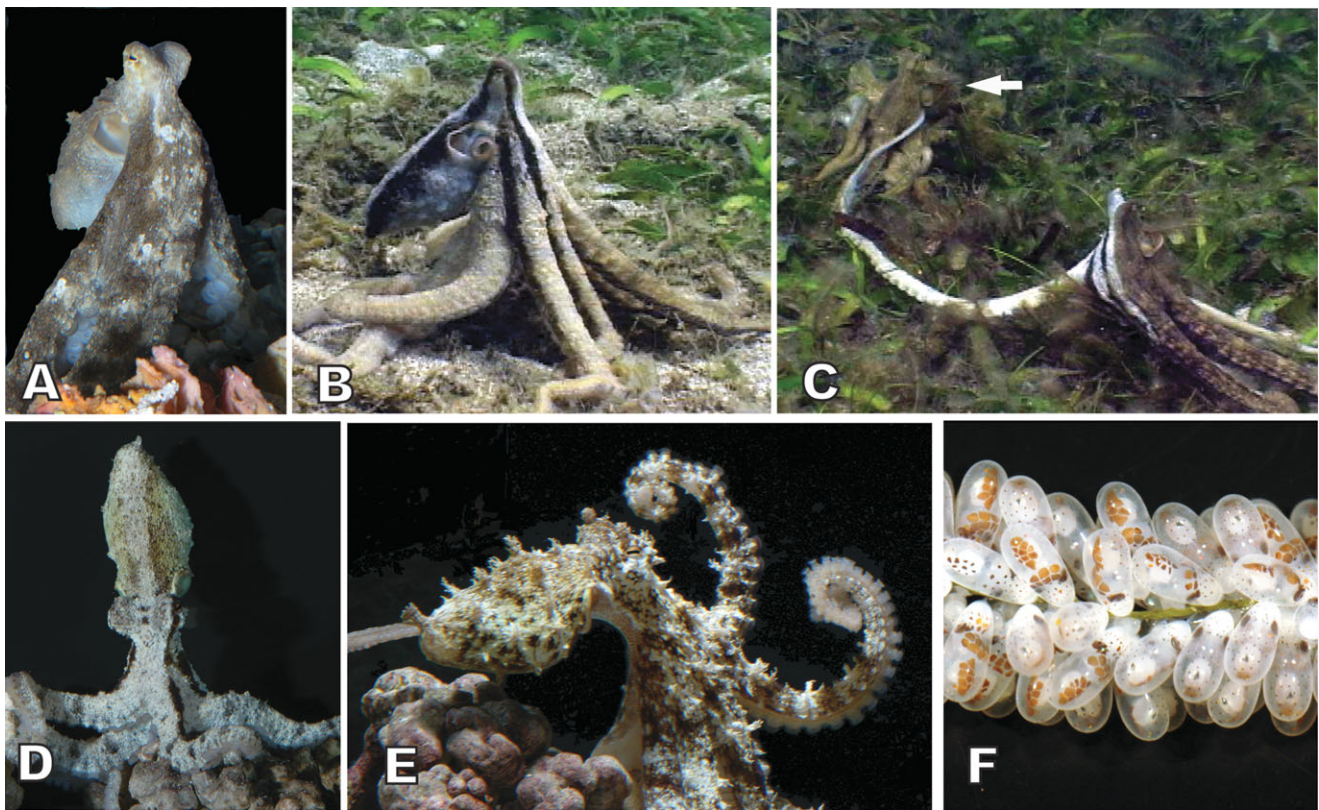


Figure 2. Mating and agonistic displays of *Abdopus aculeatus*. **A.** Male standing erect to view a conspecific; photograph by R. Caldwell. **B.** Mate-guarding male crawling *in situ* while showing a white background with dark longitudinal stripes (BWS); mantle stripe forms a complete line in this image. **C.** Mate-guarding male (lower right) and mate-guarded female (upper left) mating *in situ*; male displayed 'BWS' and raised supraocular papilla on side facing female; arrow points to camouflaged female. **D.** 'Mantle bounce display' (MBD), with mantle in raised position; photograph by R. Caldwell. **E.** Female-postural display of dorsal arms raised and curled at tips (DACT); photograph by R. Caldwell. **F.** Developing eggs (age 22 days, eggs approximately 2 mm long); photograph by R. Caldwell.

secondary papillae, branching primary papillae and exhibiting a cryptic body pattern (as in Fig. 2I); (4) 'punching' [reaching toward or contacting with the curled end of a rapidly extending arm, typically one or two of the dorsal arm pair (= 'arm pair I')], or 'whip' ['rapidly extending the arm at an opponent' (Cigliano (1993))] a straight arm (typically arms I, or adjacent arms I and II); (5) flaring the body and web while showing the dynamic display (Fig. 2D); or (6) moving from the area by crawling or jetting. Inking was observed five times out of 481 overt reactions to fish, and six times during 231 aggressive interactions with conspecifics. The ink was diffuse in North Sulawesi, but maintained its shape at all other sites.

Burying behaviour was observed only in juveniles. They buried by using oral surface of the arms to push away sand and lower the body into the substrate, with mantle positioned directly above the arm crown.

'Conical crawling' (Fig. 1J) by *A. aculeatus* resembled a crawling hermit crab and may serve as mimicry. The shape, colour and texture of the mantle resembled a gastropod shell overgrown with algae, while the dark arm bars resembled the stripes on hermit crab legs. While crawling, the arms curled back and moved forward abruptly in unison. *Abdopus aculeatus* did not exhibit the body pattern reported for hermit crab mimicry in a member of *Amphioctopus* (Tsuchiya, Yamamoto & Abe, 2002).

Agonistic interactions

Aggression was common between individuals of *A. aculeatus*, particularly males in the presence of a female. Female–female

interactions were not observed. Individuals involved in aggressive interactions approached each other via swimming, crawling, or jetting, and retreated via backward crawling or jetting. They touched the tips of the arms, 'grappled', 'whipped', inked, and/or showed BWS. On a few occasions, a large male held the end of the funnel, or wrapped one arm around the mantle opening of another individual, presumably cutting off ventilation. Male–female agonistic acts rarely lead to grappling. Cannibalism of a whole octopus was observed once when a large female captured and consumed a smaller individual, which inked profusely while trying to escape. Cannibalism of two arms by a large male might have represented the spoils of arm autotomy during an aggressive interaction. The sex and size of the consumed individual, and the owner of consumed arms, could not be determined.

Mating behaviour

Mating occurred while at dens and while foraging, between animals 30 mm ML or larger (maximum approximately 70 mm ML). All copulations were performed in the 'distance' position rather than the 'mount' position (Hanlon & Messenger, 1996), the male sometimes being dragged by the inserted hectocotylus as the female foraged (Fig. 2C). Mating typically ended with passive withdrawal of the hectocotylus.

Abdopus aculeatus exhibited multiple mating tactics. Males 'mate-guarded' females (successfully chased other males from the female with which he has mated or will mate) while foraging and while at the den. In several cases a large male occupied a

den 'adjacent' to that of a large female. Males adjacent to females mate-guarded and copulated repeatedly with those females for multiple days. These males often 'sat tall' at the den entrance while guarding (Fig. 2A). 'Sneaker matings' (matings by males that visually segregated themselves from guarding males to avoid aggression while mating) were performed by males that moved slowly, exhibited acute crypsis, and/or hid behind rocks while mating in the presence of a guarding male. Males also mated in 'transient' situations when they encountered female, but did not guard or follow her after mating.

Males displayed 'BWS' around females, although this was not considered courtship because females did not appear to respond differentially to variation in its expression. Both sexes performed a 'mantle-bounce display' during mating in which individuals sat upright, raising and lowering the mantle every few seconds (Fig. 2D). Females exhibited a display of the dorsal arms raised and curled at tips (= 'DACT') (Fig. 2E).

Brooding behaviour

We found no evidence that females relocated to another brooding site. As with a female that spawned in captivity (R.L. Caldwell & C.L. Huffard, unpubl.), adjacent females gathered a considerable amount of rubble to the entrance of their den. When they were no longer seen to emerge from the den despite nearly continuous observations in daylight hours, they were presumed to have spawned within the den.

Egg-laying was observed by two females in aquaria. Eggs were laid in branched and unbranched festoons attached at one end to the substrate. Based on differences in development, spawning appeared to occur in one bout lasting several days. Because I did not disturb the eggs to count festoons on a regular basis, I cannot confirm exact timing of spawning. One female was housed in a semi-natural situation, and she pulled a considerable amount of rubble near her, presumably to provide cover. She cloaked the festoons with the webbing between the two dorsal arms (web sector A), using the arm tips to reach underneath and clean the individual eggs.

Hatchling behaviour

Eggs (Fig. 2F) are small (approximately 2 mm) and hatchlings were planktonic.

Locomotion

Locomotion by *A. aculeatus* involved crawling, swimming, jetting and walking. Crawling with the arms sprawled around the body was the most common form of locomotion in the wild. Jetting was employed to retreat from fish and conspecifics, and to return to the den after a foraging bout. *Abdopus aculeatus* swam forward to approach conspecifics, or to capture highly mobile prey such as portunid crabs. Octopuses swam a total maximum distance of approximately 5 m, sometimes involving sudden sharp turns and reaches toward prey items in the water column. Walking may have occurred in rare occasions; however it was difficult to confirm this mode of locomotion from a distance.

DISCUSSION

Abdopus aculeatus demonstrated among the richest repertoire of skin components, body patterns and behaviours documented for any octopus. Thorough ethograms of congeners are not yet available for comparison, but based on published photographs and accounts in Norman (2000) and Norman & Finn (2001), *A. aculeatus* appears to exhibit skin components that are

expressed by several other members of the group, including a diamond configuration of (typically branched) primary papillae on the dorsal mantle, dorsal mantle white spots, lateral neck dark spots, a medial neck white spot, frontal white spots, arm white spots, dark arm bands, and a dynamic display of large pale spots on a dark background. Where known, congeners are also intertidal and primarily diurnal (Norman & Finn, 2001). Compared with other members in the genus, *A. aculeatus* (1) bears round rather than crescent-shaped dorsal mantle white spots as found in *Abdopus capricornus* (Norman, 2000; Norman & Finn, 2001); (2) does not exhibit large pale spots over the dorsal mantle during resting camouflage, and lacks elements of purple in the skin colour observed in *Abdopus abaculus* (Norman, 2000; personal observations); and (3) exhibits relatively smaller dorsal mantle and arm white spots than those expressed by *Abdopus* sp. 3 (Norman, 2000).

Abdopus aculeatus also shares several behavioural and ecological characteristics with the considerably larger *O. cyanea*. Both *O. cyanea* and *A. aculeatus* (1) are primarily diurnal; (2) forage in overlapping intertidal areas in Sulawesi, Indonesia and Lizard Island, Australia (personal observation); (3) exhibit a star-like pattern around the eye, lateral neck dark spots, transverse mantle bar and a medial neck white spot; (4) display a dynamic display of pale spots on a dark background; and (5) display dark longitudinal stripes on a pale background, with a digitate supraocular papillae during mating and aggression. As with *A. aculeatus*, large male and female *O. cyanea* sometimes occupy adjacent dens (Yarnall, 1969; Norman, 1991), males have been reported to perform sneaker matings (Tsuchiya & Uzu, 1997), and males are sometimes dragged by the hectocotylus while copulating with foraging females (D. Keisling, personal communication).

Recent phylogenetic work has found *O. cyanea* to be the sister taxon to both *A. aculeatus* and an undescribed member of *Abdopus* from Western Australia (Guzik, Norman & Crozier, 2005). If these octopuses are found to form a monophyletic group with other members of *Abdopus*, then behavioural similarities between *O. cyanea* and *A. aculeatus* likely result from their common ancestry and may be more widespread in the group. For example, an undescribed species of *Abdopus* from Guam ('sp. Ward' in Norman & Finn, 2001) can be found at moderate densities, males and females form dens near each other, and males sometimes follow females while foraging (personal observations). Formal studies in the future should consider the possibility that adjacent dens, mate guarding and sneaker matings might occur, even if they have not yet been observed.

Among the octopodids for which photographs or ethograms could be found, *A. aculeatus* appears to share the most skin components with *Octopus bimaculoides*. I do not know if these similarities reflect convergence of body patterns in animals experiencing similar selective pressures, or a shared evolutionary history. Both of these octopuses exhibit arm white spots, arm bars, arm crown stripes, transverse mantle bar, and a dynamic display of pale spots on a dark background (Forsythe & Hanlon, 1988), all of which (except the dynamic display) likely contribute to camouflage. *Abdopus aculeatus* and *O. bimaculoides* (Lang, 1997) both forage during the day in habitats comprised of mixed sand, algae and hard substrate. Their ancestors may have experienced similar selective pressures leading to the evolution of these skin components for use in crypsis. However, these similarities may also indicate a close relationship between them. Based on molecular evidence (Guzik *et al.*, 2005), *Abdopus* appears more closely related to the '*Octopus vulgaris* group' [of which *O. bimaculoides* is a member based on morphological similarity (Norman & Hochberg, 2005)] than members of *Amphioctopus*, *Hapalochlaena* and *Callistoctopus* (Guzik *et al.*, 2005). *Abdopus aculeatus* appears to share far fewer skin components with members of these latter groups. Future studies

should test whether the similar body patterns in *A. aculeatus* and *O. bimaculoides* stem from a shared ancestry or from convergence.

Although displays of light and dark longitudinal stripes or other high-contrast patterns are highly conserved in cephalopods (Messenger, 2001), they can differ discretely between species and may help with identification. Male *A. aculeatus*, *A. abaculus* (R.L. Caldwell, personal communication), *Abdopus* 'sp. Ward' (personal observation), an unidentified member of *Abdopus* from Singapore (incorrectly identified as *O. horridus*, Young, 1962), and *O. cyanea* (Wells & Wells, 1972; Van Heukelem, 1983) all display similarly striped body patterns during mating and/or aggression. Differences between these patterns include the presence/absence of dark patches on the mantle in *A. aculeatus* (Fig. 2B, C) vs. *O. cyanea* (Van Heukelem, 1983: Fig. 16), and should be explored further. In other animal groups, interspecific variation in signals can facilitate mate recognition (Ryan & Rand, 1993). On reef flats in North Sulawesi, *A. aculeatus* co-occurs with the pygmy *A. abaculus* and the giant *O. cyanea*. However, interactions between these species were not observed and it is unknown if differences in visual displays or other potential reproductive barriers such as size may facilitate mate-recognition between these octopuses.

Preliminary observations suggest that *A. aculeatus* expressed slightly more restricted activity patterns in Queensland, where predatory fish populations are protected from fishing, than *A. aculeatus* in Sulawesi, where many local predatory fish are harvested. It is unknown whether or not this variation reflects a learned understanding of environmental factors, such as predatory risk. Octopuses have long been known for their capacity to learn in laboratory situations (Boal, 1991; reviewed in Hanlon & Messenger, 1996; Fiorito *et al.*, 1998; Boal *et al.*, 2000; Hochner, Shomrat & Fiorito, 2006). The rapidity with which wild-caught octopuses learn compared to those reared in the laboratory suggests that learning occurs regularly in the wild (Boal, 1991), although to my knowledge it has been shown only during navigation (Mather, 1991b). We do not know the extent to which learning may have impacted other behaviours documented here, although it is not likely to influence skin patterns (Warren, Scheier & Riley, 1974; Messenger, 2001).

If documented in a consistent manner, behavioural characters may contribute greatly to taxonomic, systematic and evolutionary studies of octopodids. In other animal groups, nonmorphological characters (molecular: Gupta & Griffiths, 2001; behavioural: Wimberger & de Queiroz, 1996; Stuart, Hunter & Currie, 2002; developmental: Turbeville, 2002) are important for taxonomic and phylogenetic studies, particularly of animal groups deficient in distinguishing anatomic features. Octopodids share a common anatomy, have few hard parts, and several of their anatomical traits vary continuously between species (Toll, 1988; Voight, 1995). Their soft bodies distort depending on the particular means of preservation and handling (Roper & Sweeney, 1983; O'Shea, 1997; Voight, 1991a). Cephalopod biologists have long recognized that species-specific body-patterns (Packard & Hochberg, 1977; Hanlon, 1988; Ho *et al.*, 2000; Messenger, 2001) and behavioural repertoires (Hanlon, 1988) of live octopodids hold useful taxonomic cues. Behaviour and body patterns have also been used to hypothesize a close phylogenetic relationship between *O. bimaculoides* and *O. vulgaris* (Forsythe & Hanlon, 1988). While it may be difficult to use behaviour or body patterning alone to estimate octopodid relationships (theory reviewed for other animals in Stuart *et al.*, 2002), they may provide useful tools for forming preliminary hypotheses to be tested in conjunction with other methods. If detailed behavioural data are collected in a consistent manner for other species (as suggested by Hanlon, 1988, and restated here) then ethograms will be comparable across taxa, and studies can better test hypotheses about the evolution of behaviour and body patterning in this group by mapping

characters onto a phylogenetic tree and examining trait distribution [evolutionary theory discussed in Wenzel, 1992, and Stuart *et al.*, 2002; as performed for antelopes (Brashares, Garland & Arcese, 2000) and spiders (Blackledge & Gillespie, 2004)].

ACKNOWLEDGEMENTS

Financial support for fieldwork was provided by the Beim Endowment for Field Research, Sigma Xi, University of California, the Western Society of Malacologists, and the American Malacological Society. Dr Helen Fox provided airfare to Indonesia on several occasions, and Operation Wallacea provided support for fieldwork in Southeast Sulawesi. Permission to study *A. aculeatus* was granted by the Lembaga Ilmu Penelitian Indonesia (Indonesia) and the Great Barrier Reef Marine Park Authority (Australia). Farnis Boneka and Gustaf Mamangkey of Universitas Sam Ratulangi, Manado, Sulawesi provided valuable local guidance and logistical support in Indonesia. Michael Caldwell, Heather Spalding, Brendan Hever and Operation Wallacea participants volunteered their assistance in the water. Dr Mark Erdmann, Arnaz Mehta, and Tanta Ita kindly provided logistical support and language training. Fieldwork was made possible by the staffs at Bunaken National Park, Sulawesi and the Lizard Island Research Station, Queensland. R.L. Caldwell allowed use of photographs and provided invaluable advice and logistical support throughout the project. F.G. Hochberg, Sheila Patek, R.L. Caldwell and five anonymous referees provided constructive comments on several drafts of this manuscript.

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