Anti-Predator Benefits of Mixed-Species Groups of Cowtail Stingrays (*Pastinachus sephen*) and Whiprays (*Himantura uarnak*) at Rest

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Abstract

Heterospecific grouping can sometimes provide greater antipredator benefits to individuals than grouping with conspecifics. We explored the potential benefits of mixed-species group resting in the cowtail stingray, *Pastinachus sephen*, and the reticulate whipray, *Himantura uarnak*, in Shark Bay, Western Australia. From focal follow data on individual resting choice, we first ascertained that cowtails preferred to rest with heterospecifics, as they chose to settle next to whiprays more often than to pass them (with the opposite trend observed for conspecifics). In addition, we determined from filmed boat transects that cowtails formed larger hetero- than monospecific groups despite the low density of whiprays. Possible benefits accrued by the cowtail were investigated in terms of predator protection. Whiprays responded earlier than cowtails to a mock predator (boat), and were most frequently the first to respond when in a mixed group. Thus, cowtails may benefit from grouping with heterospecifics by receiving earlier warning of a predator's approach. A decoy experiment using model whiprays demonstrated that cowtails were more willing to rest with models with relatively longer tails (controlled for body size). Ray tails, which are equipped with a mechanoreceptor capable of detecting predators, may constitute an important secondary means of predator detection aside from early warning. This contention is supported by the observation that stingrays mainly form resting groups when their visual ability is likely to be impaired by environmental conditions, and that tail length is negatively allometric with body size, suggesting its importance in vulnerable early life stages. If the efficacy of the mechanoreceptor increases with tail length, then cowtails may have further improved their likelihood of detecting predators by grouping with longer-tailed heterospecifics.

Introduction

Mixed-species grouping is a widespread phenomenon found in arachnids, fish, birds and mammals (Morse 1977; Hodge & Uetz 1992; Bshary & Noë 1997; Herzing & Johnson 1997). Three main reasons have been postulated as to why such heterospecific groups are formed: (1) to improve foraging efficiency, (2) to reduce predation and (3) by chance encounters (Waser 1984; Sakai & Kohda 1995; Noë & Bshary 1997; Chapman & Chapman 2000). Because monospecific grouping can also provide foraging and anti-predator benefits, various advantages of mixed-species groups over single-species associations have been proposed. Most of these advantages stem from the differential sensory capabilities of

mixed-species groups (Morse 1977). Heterospecific groups may also be less influenced by resource competition and are therefore less costly to form than monospecific groups (Barnard & Thompson 1985). Additionally, animals may group with another species when their own numbers are limited and they require foraging or anti-predator benefits that only a certain group size can provide (Peres 1993).

The protector-species hypothesis (Pius & Leberg 1998) states that heterospecific grouping provides protective benefits to at least one species that would be unobtainable if grouped solely with conspecifics. An individual can benefit from a mixed-species association if heterospecifics are better at detecting predators (Thompson & Barnard 1983; Thompson & Thompson 1985; Fitzgibbon 1990), can defend themselves (and hence others) more successfully (Herzing & Johnson 1997; Richardson & Bolen 1999), and/or are preferentially selected by the same, common predators (Bshary & Noë 1997; Noë & Bshary 1997). Mixed-species grouping is most likely to occur when animals live in open, exposed areas where chances for concealment are rare (Wilson 2000) and the need to minimize the risk of predation is great. Additionally, if two (or more) grouping species share a common ancestry, they may overlap a great deal in their use of habitat and share similar responses to predators (Fitzgibbon 1990), thus increasing the likelihood of grouping together to obtain anti-predator benefits.

Semeniuk & Dill (2005) explored the costs and benefits of facultative grouping in a species of stingray, the cowtail ray (*Pastinachus sephen*). The results of that study revealed that cowtails form groups significantly more frequently when underwater visibility is poor because of high turbidity and/or low incident light levels. The ability to detect predators under these conditions was significantly reduced. Grouping was beneficial under these circumstances because of the protective spatial arrangement adopted by the rays (a distinct rosette formation), a significant increase in flight initiation distance, and the use of highly coordinated escape behaviours. However, grouping also had its own costs, including interference in escape between group members and significantly decreased escape speeds of grouped rays compared with solitary rays.

In this study, we investigate the possible anti-predator benefits of mixed-species grouping by two sympatric species of stingrays, the cowtail stingray (*P. sephen*) and the reticulate whipray (*Himantura uarnak*), in Shark Bay, Western Australia. This is an ideal system in which to explore the benefits of anti-

predator heterospecific grouping as the two species form groups while resting and do not engage in any foraging activity while doing so. The possibility that stingrays form heterospecific groups to increase rates of resource acquisition or to decrease foraging effort can therefore be ruled out, and resource competition is also not an issue (Semeniuk & Dill 2005). Various factors make it likely that mixed-species grouping serves primarily an anti-predator function: the resting habitat is an open shallow area where cover is unavailable and heterospecific encounters are likely. Cowtails and whiprays of all sizes are also subject to the same threats of predation in their resting habitat by bottlenose dolphins (*Tursiops aduncus*) (J. Mann, U. Georgetown, pers. comm.; C.A.D. Semeniuk, pers. obs.), carcharhinid sharks (Michael 1993; C. A. D. Semeniuk, pers. obs.), and hammerhead sharks (Sphyrnidae) (W. White, Murdoch University, pers. comm.). Being closely related (Rosenberger 2001), they share similar responses to predators (immediate escape) and thus recognize one another's anti-predator responses.

Based on observations in June 2000 that cowtails selectively join whiprays to form heterospecific groups, and given the differences in body morphology between the two ray species (whiprays have relatively longer tails; Last & Stevens 1994), we explored the possible anti-predator benefits, to the cowtail, of forming heterospecific groups with the whipray. Because grouping mainly occurred under conditions of poor visibility, in which the cowtail's ability to detect predators was visually presumed to be compromised (Semeniuk & Dill 2005), we hypothesized that cowtails intentionally group with whiprays while resting because of the superior ability of whiprays to detect predators. This might potentially arise from: (1) whiprays' as yet unmeasured greater sensory detection capability, and/or (2) the use of their very long tail (equipped with a mechano-receptor system; Maruska & Tricas 1998) to detect the approach of predators. A cowtail is thus predicted to settle preferentially next to a resting whipray when joining/forming a group. This prediction was tested by conducting focal follows of searching cowtails and recording the species with which it settled vs. the species of any ray that was passed prior to settling. Although it was not possible to ascertain whether a ray reduced its vulnerability to predation by forming mixed-species groups because no predation events were observed, it was possible to determine whether there were any differences in predator-avoidance abilities between the two species. We

therefore predicted that whiprays would respond to predators at greater distances than cowtails and respond first more frequently when in mixed-species groups. Furthermore, based on the assumption that rays with longer tails can detect predators sooner, we predicted that cowtails would be more willing to stay and rest with whiprays with relatively longer tails than with those with shorter tails. We evaluated the first prediction by investigating differences in responses to a motorboat, a mock predator. The second prediction was tested with focal follow data and by placing whipray decoys of differing tail lengths in the water and noting cowtail resting choices.

To further investigate the role of the tail as a predator detector, we measured the development of the tail as the rays grew. Our two hypotheses were that: (1) there should be a negative allometric relationship between tail length and body size because juvenile rays are presumably under a greater risk of predation than large adults and (2) whiprays should have a longer tail relative to cowtails for there to be an anti-predator benefit conferred upon cowtails forming a heterospecific group.

Methods

Study Species and Study Site

The cowtail stingray, the focal species of this study, and the reticulate whipray are closely related batoid species (Rosenberger 2001) both reaching approx. 100 cm disc width and 200 cm total length within the study area. Common inshore rays, they are known to feed on faunal invertebrates such as clams, worms, gastropods and crustaceans, and benthic teleosts (Michael 1993). Both of these ray species are widespread throughout the inshore Indo-Pacific, from Shark Bay north to the Clarence River (Last & Stevens 1994). Shark Bay, situated about 800 km north of Perth on the westernmost point of the coast of Western Australia, is a large (13 000 km^2), shallow basin comprising a series of north–south running peninsulas and islands that separate inlets and bays from each other and the Indian Ocean (Humphries 1991). Along the Eastern Bluff (S 25.80° E 113.72°), on the eastern side of Peron Peninsula, is a 2-km stretch of a shallow (≤1 m), inshore (≤20 m from the shoreline) sand flat area, where immature and adult cowtails and whiprays can be seen resting at high tide. This area is also used permanently by juvenile rays as an inshore nursery area (Fig. 1).

Stingrays have many adaptations to avoid predation while resting: raised laterally placed eyes to achieve peripheral vision (Tricas et al. 1997; Perrine 1999), burying behaviour to enhance crypsis on the sandy substrate, a lateral-line system along the entire body length to detect water movements caused by approaching predators (Maruska & Tricas 1998), a high lift coefficient of the pectoral fins for rapid take-off flights (Webb 1989), a dorso-ventrally flattened body to exploit very shallow waters, a venomous stinging spine at the base of the tail for defence and facultative grouping behaviours that result in a rosette group formation (heads pointed inwards; Semeniuk & Dill 2005). Although successful predation events were not witnessed and attempted ones rare (although observed on adult rays; C.A.D. Semeniuk, pers. obs.), the animal's perception of predation risk is still obvious in its behavioural and morphological adaptations and hence threats while at rest are a reasonable possibility (Lima & Dill 1990).

Preferred Resting Partners

To determine if cowtails selectively grouped with whiprays when resting, 15 cowtails were followed by an observer onshore (to eliminate any potential disturbance to travelling rays) on five separate days in July 2001 when they came in on the flood tide to rest. Cowtails were included in the analysis if they passed within 1 m of any resting ray, which is the extent of a ray's bioelectric detection (Tricas et al. 1995). Those that settled without passing a resting ray or were lost from sight without their final resting spot being observed were excluded. Focal follows were conducted only when underwater visibility exceeded 140 cm to ensure that focal rays could still detect a resting ray <1 m away, but in visibilities <200 cm, because beyond this range of visibility, solitary resting becomes the predominant behaviour (Semeniuk & Dill 2005). Underwater visibility was measured as the lateral distance at which an underwater observer could no longer make out the alternating black and white quarters of a 20-cm-diameter Secchi disc (Semeniuk & Dill 2005). Because of their bioelectric and other sensory abilities, it is certain that the rays were able to detect those rays that they bypassed on their way to securing a resting location. Data recorded included the number of rays passed before the focal ray settled, whether the ray rested on its own or with another ray, the size of the focal ray [categorical – small (approx. <50 cm), medium (50–65 cm), large (>65–75 cm)], the size and species
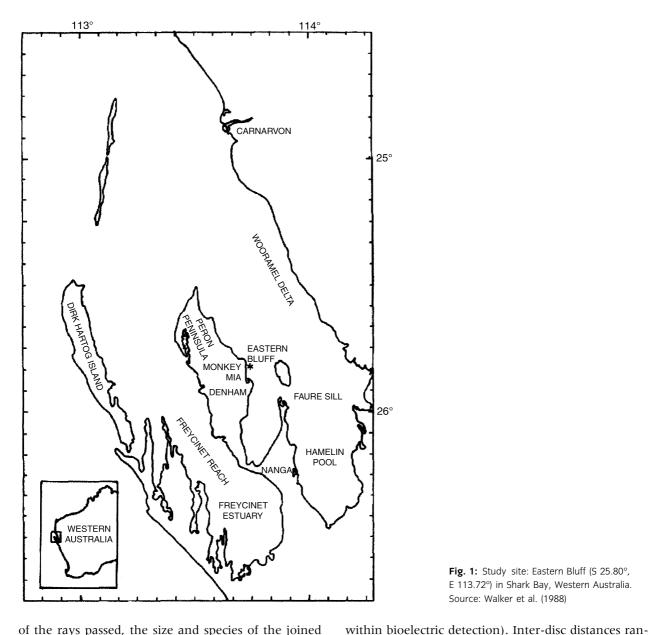
Fig. 1: Study site: Eastern Bluff (S 25.80°, E 113.72°) in Shark Bay, Western Australia. Source: Walker et al. (1988)

of the rays passed, the size and species of the joined ray(s), and any notable behaviours associated with joining a group (i.e. inspections, avoidance). Chi-square contingency tests were performed to determine whether settlement choice was dependent on species and size of the ray(s) joined.

To further investigate associations between species, mean and medium disc widths of both species were measured, and mean and typical (the group size experienced by the average individual in the population, Giraldeau 1988) single- and mixed-species group sizes were also recorded and compared. Groups were defined as two or more individuals in direct contact or with the disc of each ray being no more than 1 m away from its nearest neigbour (i.e.

within bioelectric detection). Inter-disc distances ranged from 0 to 90 cm, with a mean of 19 cm (±20.5 SD), a median of 15 cm and a mode of 0 cm (Semeniuk & Dill 2005). We conducted 14 boat transects during June and July 2001, between 1 h before and 1 h after high tide (to allow for the majority of rays to have already entered inshore and begin resting), between 09:00 and 18:00 hours. Before and after these times of day, rays were not regularly observed and were presumed to be feeding in other areas within the bay. Observational transects were accomplished using a colour, wireless, miniature video camera fastened to a 8.5-m aluminum pole affixed to the bow of a 3.36-m aluminum boat equipped with a 15-hp outboard motor. Video

data were transmitted via UHF radio to a video-cassette recorder. The camera, with a wide-angled lens attached, was positioned 6 m off the bow and 7 m high, and provided a 12-m-diameter field of view. The large field of view of the camera allowed most rays in the resting area to be captured on video, in their natural resting posture. Buried rays were easily detected by the distinct outline of their shape in the sand combined with the protrusion of their black tails, which remained unburied. Transects were conducted under conditions of poor visibility (underwater visibility index <200 cm), when grouping was predominant.

Differences in Predator-Avoidance Attributes

In an attempt to explain why whiprays are preferred resting partners under conditions of poor visibility, differences in predator-response capabilities between the two stingray species were examined. Flight initiation distances (FID) were measured from the 14 transects recorded under poor visibility as described above. The distances at which solitary and grouped cowtails and whiprays initiated flight from the research boat were compared, with each 'attack' on a solitary or grouped ray recorded by the video camera mounted on the predator boat and subsequently analysed using a frame-by-frame video player. Boat speed averaged 58 m/min (SD 9), and would cause a flight response in the stingrays at an average distance of approx. 5 m. To provide a scale and to correct for lens distortion when analysing the FID data, a 12×12 m grid was filmed separately and then traced on transparent plastic sheets and placed over the television screen when viewing the FID video footage. The distance from the bow of the boat to the centre of the ray's body disc when it initiated its escape was then recorded to an estimated resolution of ± 0.25 m. Flight initiation was defined as the moment an undulation of the ray's pectoral fin(s) was observed, seen as a flash of white as the ventral surface of the fin came into view just prior to flight. FIDs were then compared among species and group types using ANOVA, and a chi-square contingency test was used to determine if the frequency of first response to the approaching boat was dependent on species, taking into account the composition of the mixed-species groups.

Decoy Experiment

The willingness of searching cowtails to settle with decoys of different tail lengths was tested by setting out whipray cutouts of fixed size (71 cm disc width; 72 cm disc length), made from unpainted marine plywood. Decoys were lightly covered with sand and submerged by attaching lead diving weights to their underside. Decoys were fitted with a hard black plastic garden hose (0.75 cm diameter) in various lengths to mimic whipray tails: 0.61, 1.22, and 2.44 m, representing half the normal tail length, the normal tail length, and twice the normal tail length, respectively. The decoys were placed in three adjacent areas along the shore (all three tail lengths per area, randomly ordered), with decoys spaced at least 10–15 m apart, always parallel to the shoreline but oriented in either a northeastward or southeastward direction on a given day. This orientation ensured that rays travelling parallel to the shoreline would usually encounter the decoy head- or tail-on, and therefore would not be able to assess tail length without inspecting the entire decoy. Each decoy type was equally distributed among all positions (first, second, third) in the sets of three. The decoy experiment was conducted on 15 days, six in July 2000 and nine during June and July 2001 (similar grouping patterns were observed between the two years, so the data were pooled). The total number of times each tail length was placed in the water was 37, although no more than nine decoys were deployed on any given day. Decoys were set out on the rising tide and checked approximately 3 h later at peak tide. The number of cowtails within a 2-m radius around each decoy was recorded. A chi-square contingency test was used to determine whether settlement choice was dependent on encounter frequency, predicted from a random-search null model. Because all models were equally abundant, expected encounter probability would depend only on detectability (longer- and normal-tailed decoys might be four times and twice as easy to detect as half-tailed decoys respectively). This test is conservative because, as noted above, rays probably had to encounter and inspect a model in order to assess its tail length.

Tail Length Allometry

To determine how the relationship between the length (cm) of a cowtail's tail and the width of its body disc (cm) changes with age, photographs were taken using a digital Sony camcorder (Sony Corporation, New York City, NY, USA) secured to the end of a 4-m-long aluminum pole. The camera was placed directly above resting cowtails (n = 50), ranging in size from 19 to 77 cm disc width (DW). With an

assistant holding the pole and the camera in place, one of us (C.A.D.S.) then chased the resting cowtail away and placed a ruler in the recently vacated spot to provide a measure of scale. The actual width of the ray's disc was then measured from the videotape. The tail of a cowtail is characterized by a flap of skin that runs approximately two-thirds of its length, tapering off one-third before the tip of the tail. Length was therefore measured up to the end of the tail fold on the underside to rule out the effects of damage and predation to the tip of the tail of the adult, thus avoiding any biased length estimates. When no damage was obvious, total tail lengths were also measured to: (1) determine if the ratio of tail parts relative to one another was independent of body size, and (2) compare with the tail lengths of whiprays. Disc widths and tail lengths were then log_{10}-transformed to satisfy the assumptions of normality, and the latter regressed against the former.

To determine if whipray tails are longer than cowtails' for a given disc width, photographs of whiprays (20–60 cm disc width; n = 8), the entire tail lengths of which were clearly discernible in the photo image were measured from the digital Sony camcorder stills. Disc widths and tail lengths were log_{10}-transformed, regressed one against the other, and the relationship compared with that for cowtails using ANCOVA.

Results

Preferred Resting Partners

Twelve of the 15 focal cowtails rested with at least one other ray, but on average, passed two rays (±2 SD; 0–6 range, with a passed group counting as a single pass) before settling to rest. Whiprays were the preferred resting partners: only 18% of encountered cowtails were joined compared with 62% of encountered whiprays. Cowtails passed more resting cowtails (resting solitarily or in groups – which was again counted as a single pass) than expected based on relative frequency, whereas they settled with whiprays more often than they passed them ($\chi^2 = 7.6$, d.f. = 1, p = 0.006; Fig. 2).

Cowtails passed same-sized and smaller rays more often than they settled with them (with each passed ray counted, whether alone or in a group), whereas they settled with larger rays more frequently than they passed them ($\chi^2 = 16.9$, d.f. = 2, p = 0.0002; Fig. 3). Settlement choice therefore appears to occur post-encounter and is dependent on the size of the ray encountered. These findings may largely be a
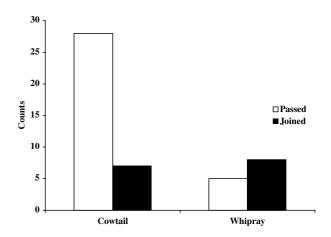

Fig. 2: The number of resting cowtail stingrays and whiprays passed and settled with by cowtails searching for resting opportunities (n = 12). A group counted as a single pass; if mixed species, it was counted once for cowtail and once for whipray
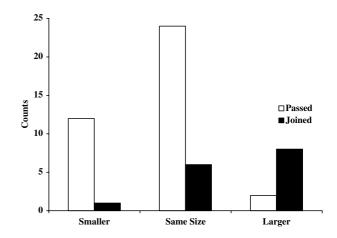

Fig. 3: The number of resting stingrays (of both species) passed and settled with that were smaller than, the same size as, or larger than the searching focal cowtail ray (n = 12). Each ray was counted, whether alone or in a group

species effect because, within the study area, whiprays were larger (mean disc diameter: 63 cm ± 11.9 (SD); median: 65 cm; n = 120) on average than cowtails (52 cm ± 7.5 (SD); median: 50 cm; n = 334; $t_{mean} = 12.2$; p = 0.0001). Controlling for disc diameter, whiprays also had relatively longer tails than cowtails (see section Tail Length Allometry, below).

Eight of the 12 rays that settled with at least one other ray exhibited obvious tail-inspection behaviour, whereby the ray would approach a resting ray (that was facing away) alongside its tail, move up the length of the tail and then position itself next to

or facing its disc. If approaching a resting ray head-on, the cowtail would pass over the ray, travel down the length of its tail, then turn around and settle next to that ray's disc. No other group member(s) were observed to leave when the focal ray settled, and this lack of avoidance indicates that observed settlement patterns are not a function of the intolerance of one species or size of ray to the arrival of another.

From the video-recorded transect data, the percentage of cowtail groups (single- and mixed-species groups) that contained whiprays (46%) was much lower than the percentage of whipray groups that contained cowtails (78%). This was probably, in part, because of the lower density of whiprays in the study area; whiprays comprised only 31.4% of the total number of rays counted during the 14 transects (519 cowtails; 238 whiprays). Despite the low density of whiprays, the average sizes for cowtail, whipray and mixed-species groups were: 2.3 ± 0.13; 95% CI (n = 95), 2.2 ± 0.26; 95% CI (n = 23), and 2.6 ± 0.26; 95% CI (n = 83) respectively. These group sizes differed significantly from one another (Kruskal–Wallis, H = 7.2, p = 0.028), with mixed-species groups being larger than both single-species cowtail (Mann–Whitney, U = 3355.5, p = 0.03) and whipray groups (U = 726.5, p = 0.035). Typical group sizes followed a similar pattern, heterospecific groups being larger than both cowtail and whipray groups (3.2, 2.5, and 2.4 respectively).

Differences in Predator-Avoidance Attributes

The rays' FID to the approaching boat differed among species and group types (Table 1; ANOVA, F = 2.6, d.f. = 3, 62, p = 0.03). Whiprays that responded first in mixed-species groups did so at greater distances than cowtails in single-species groups and cowtails who responded first in mixed-species groups (Fisher's PLSD post hoc test for these

Table 1: The mean distance ($\pm$SD) at which the first grouped ray initiated flight (FID) from the approaching boat, depending on ray species and group type

	FID (m)	n
Single-species cowtail ray groups	4.44 ± 2.34^{a}	24
Single-species whipray groups	$5.23 \pm 2.33^{a,b}$	7
Mixed-species groups; cowtail ray first to react	3.84 ± 1.06^{a}	9
Mixed-species groups; whipray first to react	5.91 ± 2.50^{b}	25

Same letter superscripts denote no significant difference; different letter superscripts denote a significant difference.

two comparisons: p < 0.03). In 34 mixed-species groups, whiprays responded first 25 times (73%), although they made up only 49% of the membership of these groups ($\chi^2 = 4.0$, d.f. = 1, p = 0.046). Moreover, the distances at which whiprays in single-species groups and in mixed-species groups (in which the whipray was the first to respond) reacted to the approaching boat were independent of disc width (min.–max. disc width: 40–110 cm; $r^2 = 0.069$, $F_{1,48} = 3.55$, p = 0.07).

Decoy Experiment

Controlling for disc width, and allowing only tail lengths to vary, more cowtails were counted next to the whipray decoy (see Fig. 4) with the longest tail (L) than the decoy with a normal-length tail (N) or the decoy with a short tail (S) (49, 25 and 9 respectively; $\chi^2 = 14.4$, d.f. = 2, p = 0.0007). This resting distribution was due to the long-tailed decoy being chosen more often as a resting partner, as the sizes of the groups formed about each decoy were statistically similar (Kruskal–Wallis, H = 0.59, d.f. = 2, p = 0.73). The mean group sizes (SD) per decoy were: long (n = 26): 2.7 (2.53), normal (n = 15): 2.5 (2.78), and short (n = 4): 2.5 (2.38). Based on their relative 'detectability', the expected proportion of decoys encountered (0.14, 0.29 and 0.57 for decoys with short, normal, and long tails respectively), did not differ significantly from the observed proportion of decoys chosen by at least one ray (0.09, 0.33 and 0.58 short-, normal- and long-tailed decoys respectively; $\chi^2 = 1.15$; d.f. = 2, p > 0.05). There was no effect of decoy orientation [i.e. decoy disc facing north-east (n = 15) or south-east (n = 22)]. Decoys in both orientations had cowtails resting next to them an equal number of times: S: $\chi^2 = 0.48$, d.f. = 1, p = 0.5; N: $\chi^2 = 0.83$, d.f. = 1, p = 0.4; and L: $\chi^2 = 0.26$, d.f. = 1, p = 0.6.

Tail Length Allometry

A significant positive relationship existed between $\log_{10}$ tail length (up to the tail fold) and $\log_{10}$ disc width for cowtails ($r^2 = 0.622$, $F_{1,48} = 78.99$, p = 0.0001). The slope of this relationship (0.591) was significantly <1 (t = 6.15, p = 0.001), denoting negative allometry (Fig. 5). Using the entire tail (when clearly visible; n = 30) gave almost identical results (slope = 0.597; $r^2 = 0.606$, $F_{1,28} = 43.08$, p = 0.0001).

For a given disc width, whiprays had significantly longer tails than cowtails (ANCOVA, log disc width:

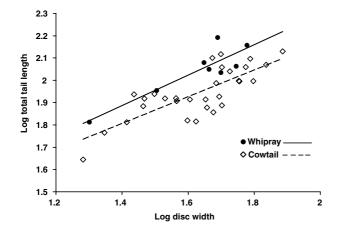**Fig. 4:** Cowtail (background) settled next to a long-tailed decoy (foreground)

Fig. 5: Log$_{10}$-transformed total tail length regressed against log$_{10}$-transformed disc width for cowtail stingrays and whiprays

Fig. 6: A mixed-species group of three showing the difference in relative tail lengths; cowtails centre and top right, whipray top left of photograph

$F_{2,35} = 63.7$, $p = 0.0001$; species: $F_{2,35} = 13.2$, $p = 0.009$; log disc width * species: $F_{3,34} = 0.24$, $p = 0.63$; Fig. 5). The relative difference in total tail lengths between a whipray and cowtail of similar disc diameter is illustrated in Fig. 6.

Discussion

This study reveals that cowtails preferentially settle with whiprays, as indicated by both focal follow observations and larger mixed-species groups, and supports the hypothesis that this predilection may be due to the relatively greater anti-predator advantages afforded by the whipray. Cowtails also preferentially settled with larger rays with longer tails, perhaps because of the increased likelihood of predator detection via the mechanoreceptor sense found along the length of the tail.

To explain the tendency of animals to form groups, gregariousness is sometimes considered a byproduct of animals using the presence (or

absence) of others as a cue to suitable resting (or foraging, etc.) microhabitats (see Childress & Herrnkind 2001 for a review). This 'guide effect' benefits the resource-seeking animal by reducing the time of exposure and hence predation risk, while increasing the time spent exploiting the resource. Rays in poor visibility conditions did not usually settle with the first ray they encountered, and hence, potentially increased their exposure to predators. This behaviour suggests that rays may not necessarily use others as evidence of a suitable resting spot, but rather actively seek out suitable resting partners for other benefits that grouping can provide.

The protector-species hypothesis holds that mixed-species groups are formed so that species with lesser ability of detecting predators can take advantage of the greater sensory capabilities of heterospecifics (Pius & Leberg 1998). This has been reported for shorebird species (Thompson & Barnard 1983; Metcalfe 1984; Thompson & Thompson 1985), fish (Sakai & Kohda 1995), primates (Peres 1993; Bshary & Noë 1997) and ungulates (Fitzgibbon 1990). Whiprays were more responsive than cowtails (whether visually or because of the noise of the boat) in terms of the distance at which they reacted to the boat irrespective of whipray size, and the frequency with which they were the first to respond in a mixed group. As cowtails respond to the flight initiation of whiprays, cowtails would be at an advantage forming these mixed-species associations. These results suggest that it is species, not size, that partly influences cowtail grouping decisions.

Incidental evidence supporting the notion that mixed-species stingray groups are formed as a means of predator avoidance comes from the observation that heterospecific groups were larger than single-species groups. Heterospecific groups are usually larger, on average, than monospecific groups (Fitzgibbon 1990) because of behavioural, ecological and/or density constraints. For instance, large single-species groups may be limited by dominance or sexual aggression, by feeding competition over limited resources, or simply by the low density of conspecifics present (Peres 1993; Bshary & Noë 1997; Herzing & Johnson 1997). However, none of these constraints apply to cowtail stingrays. While whipray density was certainly low and could explain why whiprays form larger groups with heterospecifics, it does not explain why cowtails, the more abundant species, did not form larger single-species groups themselves, despite the opportunity. In fact, had whipray density been higher, we may have observed an even higher number of large, mixed-species

groups. Nevertheless, the occurrence of larger heterospecific groups may indicate that cowtails are more willing to incur the costs of larger groups (Semeniuk & Dill 2005) because of the whipray's enhanced ability to respond to a predator, respond at greater distances, and/or detect predators sooner using other sensory modes besides vision.

In clear waters, fish primarily rely on visual cues to detect predators. When the availability of this information is reduced (e.g. by high turbidity levels), fish must detect predators using other cues. Species that inhabit more turbid waters typically have better-developed alternate sensory modes, primarily olfactory, to detect alarm signals (Hartman & Abrahams 2000). The Dasyatidae have excellent vision with which they are capable of detecting approaching predators in high-light conditions (Gruber et al. 1991; Murphy & Howland 1991; Perrine 1999), but in low-light conditions when their vision is limited, they would also need to rely on the mechano-receptor system along their own (or another's) dorsal surface and tail. This is especially important because their main predators, sharks, do not rely solely on vision to detect them, but possess an electro-receptor sense capable of detecting the rays' bioelectric signals (Kajiura & Holland 2002).

Focal cowtails did not always settle with the first larger ray encountered within their sensory range, and they passed two resting rays, on average, at distances that should easily have allowed detection of bioelectric signals; hence, an absence of electric cues or a lack of visual conspicuousness cannot explain partner choice. Although an effect of tail length on encounter probability could explain the observed proportions of decoys chosen, results from the focal follows indicate instead that decisions to stay are made post-encounter, especially because cowtails and smaller and same-sized rays were encountered more frequently than whiprays and large-sized rays (see Figs 1 and 2). Rays most likely also responded to the decoys as 'stingrays': the lead diving weights used to sink them produced an electric field large enough to be detected by elasmobranchs (G. Gibbon, U. Witwatersrand, pers. comm.), and stingrays are attracted to and respond to artificial electric dipoles as buried conspecifics in laboratory experiments (Tricas et al. 1995). Finally, the formation of 'groups' with the decoys followed the distinct rosette-formation of heads-in-tails-out observed in Semeniuk & Dill (2005; C. A. D. Semeniuk, pers. obs.). Disc width (size) is also not necessarily a robust predictor of partner choice as decoys were of equal disc width, allowing only the length of tails to vary. The most

likely explanation for the focal follow and decoy results is that cowtails recognize their buried conspecifics bioelectrically (regardless of tail size), but assess the quality of their potential resting partner with respect to predator protection on the basis of species and relative tail length. Observations of rays making 'tail inspections' of resting rays before settling with them also suggest the importance of the tail in group-joining decisions.

Further evidence consistent with the tail's role as a predator detector is the negative allometric relationship between tail length and disc width in cowtails. Such negative allometry in morphological, physiological and behavioural traits is sometimes reflective of differential predation pressures at various life stages (Pounds et al. 1983; Sisneros et al. 1998; Cromarty et al. 2000; Mondor & Roitberg 2002). Negative tail allometry with ontogeny in the cowtail may be indicative of the use of the tail as an anti-predator defence (either as an expendable body part, or as a sensory device to detect predators), which may be more crucial during earlier life stages when stingrays are likely to be more vulnerable to predation. However, this result does not negate the realized predation risk on immature and adult rays (maximum recorded disc width of only 110 cm), and their sustained anti-predator behavioural and physiological adaptations while at rest in inshore areas.

The occurrence of mixed-species grouping among stingrays in Shark Bay provides opportunities for further study. Additional research on whiprays is needed to identify their resting preferences and to determine whether they benefit at all from heterospecific associations. One possible benefit may be an increase in group size, thereby offering an increase in protection or a dilution effect, as low densities of whiprays were observed in the study area and it would be difficult for them to form large groups on their own. Additionally, the possibility that whiprays are preferred resting partners because they are preyed upon in preference cannot be ruled out. Shark Bay is a very large basin with areas varying in predation risk (i.e. protective mangroves vs. open sand flats) and it would be of interest to determine the proportion of heterospecific groups in these areas of the bay to ascertain whether heterospecific grouping varies with risk.

In most studies on single- and mixed-species associations, it is difficult to conclude whether groups are established to benefit from predator protection or increased foraging efficiency (Bohlin & Johnsson 2004). In a system where the only activity the species are engaged in is rest, conclusions can be drawn

much more readily. This study is the first instance in which the purpose of heterospecific grouping has been investigated for animals that come together only to rest, a potentially risky behaviour that necessitates anti-predator measures.

Acknowledgements

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