

Cost/benefit analysis of group and solitary resting in the cowtail stingray, *Pastinachus sephen*

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Unless a safe refuge is found where predation threats are negligible, resting poses risks for many animals, necessitating risk management strategies. The adult cowtail stingray (*Pastinachus sephen*) of Shark Bay, Western Australia, is a solitary foraging animal that facultatively groups when resting on shallow, inshore sand flats. We hypothesized that environmental conditions influence the propensity of cowtails to group due to the limited ability to detect predators visually in certain conditions. We then explored the possible benefits of grouping, such as bodily protection, early warning, and predator confusion, in conjunction with potential grouping costs, such as increased interference when initiating flight and decreased escape speeds. Our study revealed that in poor underwater visibility (due to turbidity and/or low ambient light levels), cowtails primarily rest in small groups (three rays). Tests of flight initiation distance to a mock predator demonstrated that solitary cowtail escape distances are significantly shorter in poor than in good underwater visibility conditions. As to grouping benefits, filmed boat transects revealed that cowtails most often arrange themselves in a rosette position, possibly as a means to protect their bodies and expose their tails. The first cowtail in a group initiates flight to a mock predator at a significantly greater distance than a solitary cowtail, and grouped cowtails escape an approaching boat in a significantly more cohesive manner than a simulated group of escaping individual rays. Grouped cowtails exhibit behaviors that would impede immediate flight after detection. As a result, grouped rays escape a boat at significantly slower speeds than solitary cowtails. Results from this study demonstrate that the interplay between costs and benefits of grouped and solitary resting under differing environmental conditions is driven by differences in perceived predation risk and ultimately reflected in the facultative grouping behavior of this species. *Key words*: antipredator behavior, facultative grouping, group resting, *Pastinachus sephen*, perceived predation risk, stingrays. [*Behav Ecol*]

Animals are sensitive to the risk of predation while resting, as evidenced by their choice of resting: (1) in the safest possible areas (Cowlishaw, 1997; Heithaus and Dill, 2002; Williamson, 1990), (2) cryptically (Chattopadhyay and Chattopadhyay-Sukul, 1994), (3) with their detection senses oriented toward the most likely direction of approach by a predator (Halkin, 1983; Mulhare and Maignan, 1998), and/or (4) in groups (Fox and Mitchell, 1997; Poulle et al., 1994). Abundant evidence across a variety of taxa suggests that grouping is an advantageous antipredator strategy for an individual (e.g., Fitzgibbon, 1990; Kenward, 1978; Morgan and Godin, 1985; Morse, 1977). The increased probability of survival of an individual within a group can be accomplished by various means: protective cover, increased corporate vigilance, cooperative defense, the dilution effect, and the Trafalgar effect (see Krause and Ruxton, 2002, for a review). Although grouping can be an effective antipredator strategy, not all individuals are found in groups; some groups are maintained at sizes well below their predicted optimum (Steenbeek and van Schaik, 2001), and some animals group only under certain conditions. Such evidence suggests that there are costs associated with the formation of groups, including increased conspicuousness, increased competition for resources, increased levels of aggression, and increased exposure to parasites or disease agents (Banks, 2001; Hobson, 1978; Prokopy and Roitberg, 2001; Pulliam and Caraco, 1984; Rasa, 1997). Indeed, the interplay between the costs and benefits of group living is reflected in the extent to which

many species group facultatively, that is, only when the benefits of doing so are presumed to outweigh the benefits of remaining solitary (e.g., Rasa, 1997; Seghers, 1981).

In a social species, the decision to form a group will often be contextual, with individuals being attracted to conspecifics under certain circumstances and repelled under others. Many animals are less aggregated when resources are scarce (Dudzinski et al., 1969) or when predation risk is reduced (Beecham and Farnsworth, 1999; Ydenberg and Dill, 1986). Although competition for limited resources is usually cited as the reason for the maintenance of solitary behaviors of facultatively grouping animals (e.g., the desert tenebrionid beetle, *Parastizopus armaticeps* [Rasa, 1997], the spottail shiner, *Notropis hudsonius* [Seghers, 1981], and *Phrynomantis microps* tadpoles [Spieler, 2003]), animals may choose to be solitary due to direct costs induced by the act of grouping itself.

The purpose of this paper is to explore the facultative grouping behavior of the cowtail stingray (*Pastinachus sephen*) as an antipredator strategy while at rest and to examine the costs and benefits of group resting. The cowtail is a common inshore ray species in the Indo-Pacific and is most common in the northern half of Australia, from Shark Bay, Western Australia, to the Clarence River, New South Wales. It is a large species reaching an adult disc width of at least 180 cm and a total length of 300 cm (Last and Stevens, 1994). Along the east coast of the Peron Peninsula in Shark Bay (25.80° S, 113.72° E), this stingray rests on shallow-water inshore sand flats. Cowtails individually enter the flats on the flood tide to rest for a minimum of 4 h (Semeniuk, personal observation), leaving on the ebb tide, singly as well, presumably to feed. They group facultatively while at rest. Cowtails are at risk of predation from various shark species (Sphyrnidae and Carcharhinidae spp.) as well as from bottlenose dolphins (*Tursiops aduncus*) in the shallows (Semeniuk, personal

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observation; White W and Mann J, personal communication). This study is novel in that it explicitly investigates the benefits and costs associated with a facultative grouping behavior within the context of resting. Cowtails make an ideal study species for such an investigation as they group facultatively, are large and highly visible, rest in shallow waters where they are easy to observe, and do not engage in other activities such as feeding or mating while at rest.

The underlying assumption on which this study is based is that cowtails group for antipredator reasons. The observation of facultative grouping in cowtails under certain environmental conditions during a pilot season in winter 2000 led us to hypothesize that the ability of resting cowtails to detect an approaching predator is diminished under poor underwater visibility conditions. Consequently, we hypothesize that group resting under poor underwater visibility is beneficial because one or more attributes of escape are enhanced. Grouped cowtails are predicted to have (1) an advantageous spatial arrangement (for protection), (2) greater response distances to an approaching predator, and (3) coordinated escape trajectories, after the initial response, that could potentially confuse a predator. Conversely, other attributes of escape behavior are hypothesized to be compromised by grouping, such that if predators can be detected from afar, solitary resting is a better option. A grouped ray is therefore predicted to have its initial escape ability hindered by its resting partners also attempting to flee, thus potentially increasing its vulnerability to capture above and beyond any dilution effect.

We also consider an alternative hypothesis to explain facultative grouping: grouping is the preferred behavior under all conditions, but good underwater visibility causes cowtails to become conspicuous to predators when searching for conspecifics. Therefore, the only safe circumstance to seek out and join a group would be in those underwater visibility conditions when a predator's visual ability is hampered. Although the actual cost of searching for a group to join was not possible to quantify, we predicted that if searching for a group is risky, a cowtail in good underwater visibility conditions should (1) travel a shorter distance and/or for a shorter time before settling and (2) settle next to an already-resting ray as soon as one is encountered.

METHODS

Facultative grouping behavior

All observations and experiments were conducted along the east coast of the Peron Peninsula in Shark Bay (25.80° S, 113.72° E), Western Australia. Filmed transects were conducted during June and July 2001. Transects were performed almost every other day (barring strong winds) in an attempt to encompass all types of environmental conditions. The longest number of consecutive days without filming was five. As cowtails were not observed resting in waters deeper than 1 m or further than 15 m offshore, only a single transect was required to cover the resting area. The same transect was traversed once a day in a southward direction over the 2-km-long stretch. Each transect lasted approximately 35 min and was initiated from 1 h before to 1 h after high tide between 0900 and 1800 h. Before and after these times of day, cowtails were not regularly observed and were presumed to be feeding elsewhere. Observational transects were accomplished using a color, wireless, miniature video camera with a 900 MHz transmitter fastened to an 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 ultrahigh frequency radio to a videocassette 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-diam field of view. The large field of view of the camera allowed most cowtails in the resting area to be captured on film and in their natural resting posture. Buried cowtails were detected by the outline of their shape in the sand combined with the protrusion of their black tails, which remained unburied. Boat speed averaged 58 m min⁻¹ (± 9 m min⁻¹ SD), and the boat would cause a flight response at an average distance of approximately 5 m. Due to the raised lateral placement of their eyes, stingrays are believed to possess a complete panoramic field of view (Bodznick, 1991), ensuring a consistent escape behavior despite the angle of predator attack. We assume that the transect samples do not include significant pseudoreplication. First, the maximum number of cowtails per transect was 82; this number represents but a small proportion of the total population present in the 13,000-km² bay. Second, grouping behaviors were expressed consistently over 2 years of observation, and hence, if one allows for the effect of demographic processes, these were not entirely the same set of individuals. Lastly, the average number of cowtails in each transect varied greatly, creating a continuous fluctuation of individual composition. Therefore, we conclude that the same individuals were not sampled repeatedly.

Abiotic and biotic factors were recorded at the time of each transect. These included (1) incident light level (measured in lux using a Gossen Mastersix light meter placed at the water surface), (2) underwater visibility, quantified as the visibility index (VI) (the lateral distance [cm] at which an underwater observer [of constant identity] can just make out the alternating black and white quadrants of a 20-cm-diam secchi disc; Steel and Neuhauser, 2002), (3) percent cloud cover (estimated), (4) and (5) wind speed and wave height, respectively (ranked from 1 to 4 with increasing intensity), (6) water depth (cm), (7) the distance of each cowtail from shore (m), (8) the total number of cowtails present on the transect, and (9) the total number of (reticulated) whiprays (*Himantura uarnak*) on the transect (cowtails also group with these). To determine the most significant environmental variables affecting the proportion of cowtails found in groups, a stepwise linear regression (JMP IN, 2000) with forward elimination of non-significant variables was used to investigate the main effects and their interactions.

Groups (single-species cowtail or mixed species) were defined as two or more individuals with the disc of each ray being no more than 1 m away from its nearest neighbour (i.e., within bioelectric detection, Tricas et al., 1995). Rays whose tails would overlap, regardless of interdisc spacing, were also considered a group (as predator information could also be transmitted through touch). The positioning of rays within groups and the interdisc spacing between adjacent group members (measured from the rays' disc edges) were also documented, and the frequency distribution of different group sizes was determined and compared to a Poisson distribution to test for randomness (Zar, 1984).

Effect of environmental variables on flight response

We measured the flight response of solitary, resting cowtails (50–60-cm disc width) to an approaching 2-m-long mock hammerhead shark under as many different underwater visibility conditions as possible. The predator model was made of Styrofoam, wire mesh and mattress foam, and had a 2.67-m-long polyvinyl chloride pipe attached at the rear. The pipe was used by C.A.D.S. (in the water) to move the predator in a side-to-side manner to mimic the anguilliform movement of a swimming shark. Beginning at least 15 m from the resting cowtail, the mock predator advanced on each cowtail head-on at a speed of 0.5 m s⁻¹, previously practiced until consistent.

An assistant, at least 3.5 m away, filmed the target cowtail using a Sony digital camcorder mounted on a 4-m-long aluminum pole and held over the ray. This was done for the purpose of recording any preflight response to the predator in hopes of differentiating between detection and response (Ydenberg and Dill, 1986). As soon as the cowtail initiated its escape or immediately afterward the following variables were measured: flight initiation distance (FID, cm), incident light level (lx), VI (cm), temperature ($^{\circ}\text{C}$), percent cloud cover, wind speed and wave height (ranked), water depth (cm), the distance of the cowtail from shore (m), and Julian date. A stepwise linear regression (JMP IN, 2000) with forward elimination of nonsignificant variables was used to investigate which environmental conditions and their interactions most affected the FID.

Benefits of grouping

Early warning

In addition to measuring the FIDs of solitary cowtails to a mock hammerhead shark in various environmental conditions (see previous section), mixed- and single-species groups of different sizes (2–6) were also approached, and the FID of the first cowtail in the group to initiate escape was recorded. Only groups in which a cowtail was the first ray to initiate flight were used. Response distances were then compared between solitary and grouped cowtails under various underwater visibility conditions using an analysis of covariance (ANCOVA) with group size as a covariate.

Concerted escape

From filmed transects in both poor and good underwater visibilities in which cowtails were startled by the boat, the mean escape trajectory of solitary cowtails and the overall mean escape trajectory vector of grouped rays (each group contributed only its mean trajectory to the data set) were calculated and tested for uniformity about 360° using circular statistics (Batschelet, 1981). Escape trajectory was defined as a circular variable, with 0° as the direction to the shoreline (for reference) and 90° as the direction of stimulus approach (the boat traveling in a 90° to 270° direction), and measured in 22.5° bins. Initial orientations of resting cowtails (both solitary and grouped individuals) to the boat and relative to the shoreline were also tested for uniformity to determine whether any nonuniform initial orientation was responsible for the escape trajectory chosen. If any distributions were nonuniform, the mean initial orientation vector was compared to the mean escape trajectory vector using a Watson's F test (Kovach, 1994) to ascertain if cowtails were escaping in the same direction they were facing at rest.

To determine if grouped rays escaped in a concerted fashion, the angular dispersion of the animals' ultimate escape direction was calculated for each group from transects filmed in poor underwater visibility conditions only (to rule out bias from grouped cowtails in good underwater visibility, in which resting solitarily is the norm). The length of the mean vector of a circular variable (r) is a measure of concentration, and $1 - r$ is a measure of dispersion (Zar, 1984). Having a measure of dispersion approaching 0 indicates concentration, whereas a value of 1 indicates maximum dispersion. We compared our observed measures to the dispersion calculated for 300 computer-simulated groups of three "rays" (the typical group size) in which each ray was allowed to escape randomly in any angular direction (22.5° bins). Group-member dispersion was also compared to that of actual escaping solitary cowtails ($n = 100$), whose trajectory data were randomly assorted with replacement into groups of three, with each individual allowed to escape in their

recorded direction, and also computer simulated 300 times. Solitary cowtails were drawn from good underwater visibility conditions so as to use an unbiased data set. We carried out this latter comparison to try to determine if escape is deliberately coordinated among group members or is the result of a shared escape trajectory preference of single cowtails. The three mean angular dispersion values were compared using ANOVA with post hoc Fisher's protected least significant difference (PLSD) comparisons to determine if grouped rays escaped in a random or more (or less) coordinated fashion and if their escape pattern mimicked that of artificially grouped solitary cowtails.

Costs of grouping

Interference behaviors

Once a grouped cowtail began its escape, we recorded factors that could hinder the escape of its fellow group members. Such factors included (1) creation of a thick cloud of sand while fleeing; (2) overlap of discs, impeding the underlying ray's escape (the bottom ray could often be observed struggling); (3) blocking of the intended trajectory of the other rays' escape, causing a switch in trajectory angles by at least 45° ; (4) blocking of the intended trajectory of the other rays' escape, causing a reduction in speed to avoid a collision; (5) crossing over of another cowtail; and (6) actual collision with another escaping ray.

Decreased escape speeds

Differences in escape speeds between solitary cowtails and grouped rays were measured in response to the boat. Because the escape responses of resting cowtails to the boat during observational transects were similar to those observed when dolphins and carcharhinid sharks approached (Semeniuk, personal observation), the boat was considered to be an adequate predatory stimulus. Each such "attack" on a ray was filmed and subsequently analyzed frame by frame. To provide a scale and to correct for lens distortions and refraction, a 12×12 -m wooden grid with marked 1-m intervals was filmed in a swimming pool at three depths (30, 60, and 90 cm) with the camera positioned at a fixed height identical to its original position on the boat. Each depth grid was then individually traced onto a transparent plastic sheet and placed over the television screen when viewing the video footage of transects recorded for that depth ± 15 cm. The distance each solitary cowtail and grouped ray traveled in 3 s (150 frames) was measured to reflect acceleration from rest combined with subsequent terminal velocity; meter per second was not calculated as maximum constant velocity was not yet attained. The distance between the bow of the boat and the ray when it initiated escape was also recorded to control for any effect of predator distance on escape speed. Escape speeds of both solitary cowtails and whiprays were compared with ANCOVA, using FID (m) and size of ray (disc width, cm) as covariates, to determine if species could be pooled when investigating average escape speeds of mixed groups. Differences in escape speeds between solitary cowtails and grouped rays (single-species cowtail and mixed species combined) were subsequently compared using ANCOVA.

Alternative costs to grouping

To determine whether a cowtail perceived good underwater visibility conditions as risky, we measured the tendency of an arriving cowtail to settle with other rays encountered resting. Focal follows were conducted from the shore on individual cowtails when they came in on the flood tide to rest. Due to the slope of the shore, cowtails were spotted without visual

Table 1

Stepwise linear regression model summary of the significant and nonsignificant environmental variables used to explain the proportion of cownail rays found in groups ($n = 29$ transects)

Parameter	<i>F</i> statistic	<i>p</i> value
Number of whipsrays/transect	14.5	<.001
Number of cownails/transect	0.6	.46
VI (cm)	13.6	.001
Incident light (lx)	0.4	.56
Wind speed (ranked)	0.4	.52
Wave height (ranked)	0.9	.36
Distance of cownail from shore (m)	0.6	.09
Water depth (cm)	0.5	.46

No higher order interactions were significant and excluded from the model.

aids within 10 m of the shore in less than 1-m water depth. They were included in the analysis if they passed within 1 m of a resting ray. Cownails that settled without passing a resting ray or were lost from sight (which occurred with equal frequency in good and poor underwater visibilities) were excluded from the analysis. Focal follows were conducted at VIs no less than 140 cm in an attempt to ensure that focal cownails could still detect a resting ray less than 1 m away. In the absence of information, to the contrary, we assumed that the limits of a cownail's visual ability are similar to our own. Rays are also capable of detecting buried conspecifics within a meter using their electrosensory system (Tricas et al., 1995), so rays bypassed at that distance should have been detectable visually or electrically. Data recorded included the distance traveled (m), the time spent traveling (min), the number of rays passed (within 1 m) before the focal cownail settled, the proximity to passed rays, whether the cownail rested on its own or with another ray, the distance to the nearest resting ray (not part of a group) once settled, and the VI. Comparisons were then made between good and poor underwater visibility conditions using contingency tests and directional *t* tests (e.g., solitary rays should travel shorter distances and durations when traveling in good underwater visibility conditions).

Statistical analyses

Statistical analyses were performed using JMP IN version 4.0 software (JMP IN, 2000) for multiple regressions and Statview software (SAS Institute, 1998) for all other noncircular statistical tests. Circular statistical tests were performed using Oriana software (Kovach, 1994). All data were tested for normality and homoscedasticity prior to analysis (nonnormal data: mean group sizes [including and excluding solitary cownails]), and nonparametric tests were then used (Mann-Whitney *U* test) when appropriate.

RESULTS

Facultative grouping behavior

A total of 29 transects were performed in various weather and water conditions. The environmental variables significantly influencing the proportion of cownails found in groups were (1) whipsray density ($F_{8,21} = 14.5, p = .0008$; positive effect) and (2) VI ($F_{8,21} = 13.6, p = .001$; negative effect; Table 1). Below a VI of 200 cm, cownails significantly increased their grouping behavior from 27% to more than 63% ($\chi^2 = 7.6, df = 1, p = .006, n = 29$ transects), and 200-cm VI was henceforth used (regardless of incident light levels) to differentiate good from poor underwater visibility conditions when analyzing the benefits (protective spatial arrangement and concerted escape) and

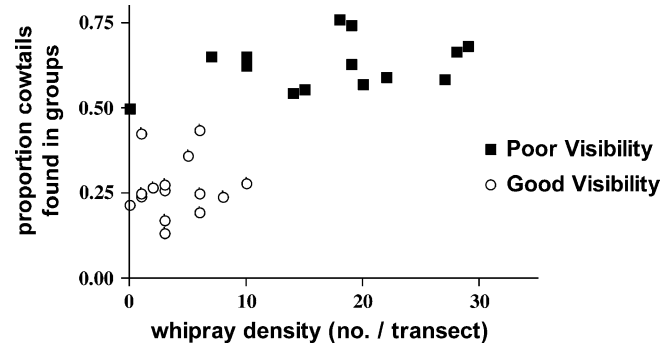


Figure 1

Scatterplot of the proportion of cownail rays found in groups as a function of whipsray density (number of whipsrays per transect) in poor (≤ 200 cm VI) and good (> 200 cm VI) underwater visibility conditions.

costs of grouping. Because no boat transects were performed in high VI (> 200 cm) with low incident light levels ($\leq 15,000$ lx), a greater resolution of environmental condition categories could not be made, unlike for the FID analyses (factors affecting escape response and early warning benefits) with the mock predator (see below), in which conditions include both high and low VI and incident light levels.

There was no significant interaction between VI and whipsray density on proportion grouped; moreover, within an underwater visibility category (poor visibility [≤ 200 cm VI] and good visibility [> 200 cm VI]), there was no effect of whipsray density on proportion of cownails found in groups (linear regression—poor visibility: $r^2 = .185, p = .12, n = 14$ transects; good visibility: $r^2 = .008, p = .75, n = 15$ transects). The effect of whipsray density arose simply because more whipsrays were present under poor underwater visibility conditions (Figure 1).

The typical group size (the group size experienced by the average individual in the population, Giraldeau, 1988) increased from good underwater visibility to poor underwater visibility whether solitaires were included or excluded. Mean group size also increased from good to poor underwater visibility but only when solitary cownails were included (Table 2). In addition, the group size distributions under conditions of good and poor underwater visibility differed significantly from one another ($\chi^2 = 104.3, df = 2, p < .001$, comparing group sizes 1, 2, and 3+). The frequency distributions of group sizes (solitary whipsrays and single-species whipsray groups excluded) for 624 rays in poor underwater visibility and 508 rays in good underwater visibility differed from a random Poisson distribution by having fewer larger groups and more solitaires than expected ($\chi^2 = 47.0, df = 4, p < .001$; $\chi^2 = 182.5, df = 4, p < .001$, for poor and good visibility conditions, respectively). However, this discrepancy was greater for group sizes in good underwater visibility (Figure 2).

Effect of environmental variables on flight response

Variables found to influence a solitary cownail's FID ($n = 43$) were (1) VI ($F_{10,38} = 14.71, p = .0002$; positive effect), (2) incident light level ($F_{10,38} = 13.14, p = .0008$; positive effect), and (3) percent cloud cover ($F_{10,38} = 6.01, p = .02$; negative effect). VI and incident light level significantly interact with one another as well (VI \times incident light level: $F_{10,38} = 13.01, p = .0009$; Table 3). The VI is somewhat influenced by (and hence incorporates) incident light levels and amount of cloud cover. However, this relationship is not a consistent one: owing to water turbidity, low VIs were recorded at times of high light and no cloud cover and high indices at times with low levels of

Table 2

Observed number of cowtail and whipray stingrays and mean and typical group sizes (including both species) in poor (≤ 200 cm VI) and good (> 200 cm VI) underwater visibility conditions

	Poor visibility ($n = 14$ transects)	Good visibility ($n = 15$ transects)	Test statistic	p value
Mean number of cowtail rays ($\pm 95\%$ CI)	37 (± 12)	33 (± 5)	0.70	.49 ^a
Mean number of whiprays ($\pm 95\%$ CI)	17 (± 5)	4 (± 2)	5.74	.001 ^a
Mean group size ($\pm 95\%$ CI) (including solitaries)	1.8 (± 0.11)	1.2 (± 0.05)	8.89	<.001 ^b
Mean group size ($\pm 95\%$ CI) (excluding solitaries)	2.5 (± 0.14)	2.2 (± 0.11)	1.12	.3 ^b
Typical group size ^c (including solitaries)	2.3	1.4	NA	NA
Typical group size ^c (excluding solitaries)	2.8	2.3	NA	NA

^a Unpaired t test.

^b Mann-Whitney U test (z value reported).

^c The group size experienced by the average individual in the population (Giraldeau, 1988).
NA, not applicable.

incident light. Exploring further the effects of incident light and VI, a comparison of FIDs between four categories of combined high and low light levels ($> 15,000$ and $\leq 15,000$ lx) with high and low VI (> 200 and ≤ 200 cm) indicated that FID was significantly affected by visibility condition (ANOVA: $F_{3,39} = 17.62$, $p = .0001$) and was significantly greater in high light/high VI than in the other categories (Fisher's PLSD post hoc test: $p < .001$ for all comparisons involving high light/high VI, and $p > .42$ for all other comparisons; Figure 3).

Benefits of grouping

Protective spatial arrangement

From the transect video footage, we noted that the positioning of rays within a group in poor underwater visibility conditions was frequently rosettelike or "marguerite" (Nishiwaki, 1962). Rosette formations are defined as groups of rays whose heads are oriented toward one another and whose tails point outward. Eighty-two percent of groups of size 2 were in a rosette formation ($n = 87$), as were 74% of groups of three ($n = 35$) and 80% of groups of four ($n = 15$). Interdisc 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.

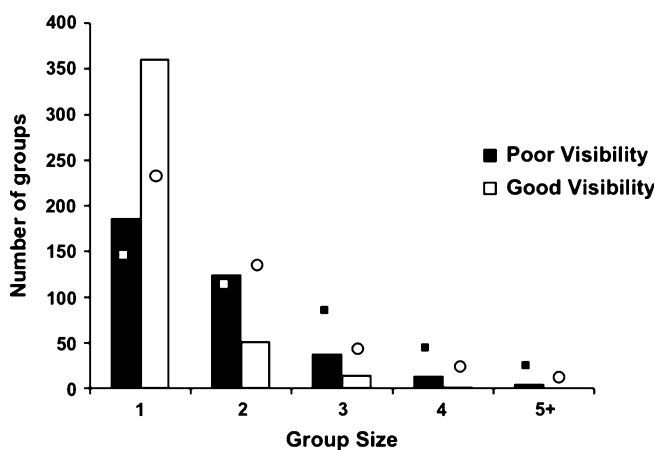


Figure 2

Size frequency distributions of single-species cowtail and mixed-species (cowtail and whipray) groups in poor and good underwater visibility conditions (see Figure 1 for definition). Squares and circles denote expected Poisson frequency distributions of group sizes in poor and good underwater visibility conditions, respectively.

Early warning

FID to an approaching mock hammerhead shark predator increased with increasing VI and increasing incident light levels for both solitary ($n = 43$) and grouped rays (single-species cowtails or mixed-species, cowtails first to respond; $n = 22$ groups) (ANCOVA, VI: $F_{3,61} = 29.6$, $p = .0001$; incident light level: $F_{3,61} = 7.7$, $p = .007$), with groups escaping at significantly greater distances than solitaries (ANCOVA, group size: $F_{3,61} = 5.8$, $p = .02$). No higher order interactions were present. Grouped rays escaped from approximately 50 cm further away than solitaries (least squared means correcting for both VI and incident light—group: $222.4 \text{ cm} \pm 32.0$ CI; solitary: $174.1 \text{ cm} \pm 22.3$ CI; Figure 4).

Concerted escape

The escape trajectories of solitary cowtails in both good ($n = 106$) and poor ($n = 83$) underwater visibility conditions were nonuniformly distributed with mean trajectory vectors of 37.2° (mode of 45° ; Figure 5a) and 29.5° (mode of 45°) away from the shoreline (0°), respectively, with the boat approaching parallel to the shore (Rayleigh test of uniformity: $z_{\text{good};0.05,106} = 75.3$; $z_{\text{poor};0.05,83} = 50.6$; $p = .001$ for both underwater visibility conditions, denoting nonuniformity).

The overall mean escape trajectory vector of grouped rays (single-species cowtails and mixed species) in both good ($n = 18$ groups; three mixed-species groups) and poor ($n = 53$ groups; 18 mixed-species groups) visibility conditions was

Table 3

Stepwise linear regression model summary of the significant and nonsignificant environmental variables used to explain solitary cowtail FIDs (cm) ($n = 43$ cowtails)

Parameter	F statistic	p value
Julian date	1.49	.23
VI (cm)	14.71	<.001
Incident light (lx)	13.06	<.001
Cloud cover (%)	6.01	.02
Wind speed (ranked)	0.51	.48
Wave height (ranked)	0.09	.76
Distance of cowtail from shore (m)	0.09	.77
Water depth (cm)	0.02	.88
Temperature ($^\circ\text{C}$)	0.01	.99
VI \times incident light	13.01	<.001

Only one higher order interaction was significant and is included in the model.

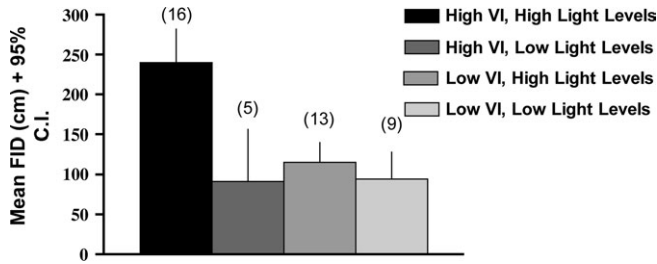


Figure 3
Solitary cowtail FID (mean FID + 95% CI) to an approaching mock predator under various environmental conditions. Bars with the same letter do not differ significantly; ANOVA with post hoc Fisher's PLSD comparisons. High VI: >200 cm underwater lateral visibility; low VI: ≤200 cm; high light levels: >15,000 lx; low light levels: ≤15,000 lx. Numbers above bars indicate sample size.

nonuniformly distributed as well (Rayleigh test of uniformity: $z_{\text{good};0.05,106} = 39.5$; $z_{\text{poor};0.05,83} = 78.0$; $p = .001$ for both underwater visibility conditions), with mean trajectory vectors of 28.5° (mode of 45°) and 14.3° (mode of 45° ; Figure 5b) away from the shoreline.

The concentrated flight direction for solitary cowtails and grouped rays under poor underwater visibility conditions was not simply a consequence of the rays' initial orientation as they were uniformly distributed relative to the shoreline and boat prior to flight (Rayleigh test of uniformity for orientation to shoreline and boat: all $z < 16.0$; $p > .05$). Solitary cowtails and grouped rays in good underwater visibility conditions were not uniformly distributed relative to the shoreline (solitary: $n = 106$, mean orientation vector = 139.3° , Rayleigh test: $z_{0.05,106} = 21.3$, $p = .01$; group: $n = 52$, mean orientation vector = 103.2° , Rayleigh test: $z_{0.05,52} = 39.2$, $p = .01$). However, rays did not escape in the same direction as they were initially oriented as mean escape vectors differed significantly from mean initial orientation vectors (solitary: $F = 35.4$, $p = .01$; group: $F = 57.9$, $p = .01$).

Because group members escaped within a mean of 0.81 s (± 0.74 s SD; $n = 52$) of one another in poor underwater visibility conditions, grouped rays were considered to initiate escape concurrently. In poor underwater visibility conditions, there was a significant difference in the escape dispersion of rays in groups ($n = 53$ groups) when compared to simulated groups of rays ($n = 300$ groups) and groups of randomly assembled solitary cowtails ($n = 300$ groups) (ANOVA, $F_{2,650} = 101.2$, $p < .0001$). The escape trajectories of group members were more concentrated (less dispersed) than simulated groups (Fisher's PLSD post hoc test; $p < .0001$), having mean angular dispersions of 0.16 (± 0.06 CI) and 0.47 (± 0.03 CI), respectively. Grouped rays also escaped slightly more concertedly than groups of randomly assembled solitary cowtails (Fisher's PLSD post hoc test; $p = .045$), whose mean angular dispersion was 0.22 (± 0.03 CI). The mean escape trajectory vector of grouped rays was also significantly different from that of the simulated groups (14.3° versus 82.6° from the shoreline for real and artificial groups, respectively; Watson's F test of the comparison of means, $F = 18.4$, $p < .0001$) and from that of the artificially grouped solitary rays ($F = 15.9$, $p < .0001$), whose overall mean escape trajectory vector was non-uniformly distributed at 34.6° from the shoreline (Rayleigh test of uniformity: $z_{0.05,300} = 282.5$, $p = .001$).

Costs of grouping

Interference behaviors

Fifty-eight percent of the 64 groups observed in poor underwater visibility conditions had noticeable behaviors

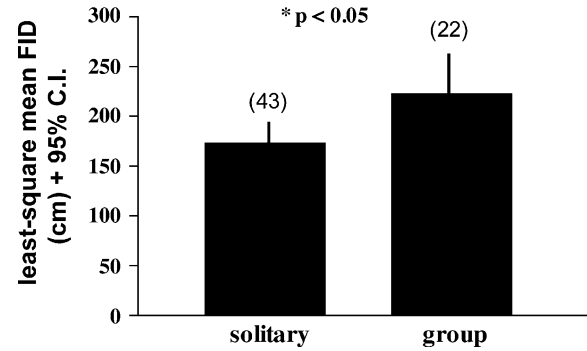


Figure 4
Least squared mean FID (FID + 95% CI) of solitary and grouped cowtails to the approaching mock hammerhead predator correcting for both underwater VI and incident light level (lx). Numbers above bars indicate sample size.

that could affect escape of conspecifics. Even in good underwater visibility conditions, 57% of the groups ($n = 58$) experienced the same potential grouping costs. Switching escape angle from the initial trajectory by at least 45° to avoid a collision with another ray (cowtail or whipray) was the most frequently observed behavior (Figure 6). Switching usually required the cowtail to decrease the distance between the boat and itself and often reduced its initial escape speed.

Decreased escape speeds

Escape speeds of solitary cowtails ($n = 57$) and whiprays ($n = 15$) were similar, and both increased with decreasing FID regardless of body size (ANCOVA, FID: $F_{3,68} = 13.26$, $p = .0005$; size: $F_{3,68} = 0.59$, $p = .44$; ray species: $F_{3,68} = 2.15$, $p = .15$; FID \times size: $F_{4,67} = 2.88$, $p = .09$). Therefore, the average escape speed of groups of rays was calculated from a data set including both single-species (cowtails) and mixed-species groups. Grouped rays escaped at significantly lower speeds than solitary cowtails in both good (ANCOVA, $F_{2,106} = 18.1$, $p < .001$; group: $n = 22$, solitary: $n = 87$) and poor (ANCOVA, $F_{2,99} = 13.8$, $p < .001$; group: $n = 45$, solitary: $n = 57$) underwater visibility conditions; however, there was no significant difference in escape speeds of groups of two to three rays and groups of four or more in poor underwater visibility (ANCOVA, $F_{2,49} = 0.16$, $p = .9$; Table 4) (there were no groups larger than three in good underwater visibility conditions). The speed of the fastest grouped cowtail stingray was not significantly different from that of a solitary cowtail in poor underwater visibility (ANCOVA, $F_{2,94} = 0.841$, $p = .36$).

Alternative costs to grouping

Fifteen cowtails were followed in each of poor and good underwater visibility conditions (Table 5). Focal cowtails, regardless of visibility condition, had the same opportunity to settle with other rays (cowtails or whiprays) as each passed by the same average number of already-resting rays (a group was counted as a single pass; $t = 0.38$; $p = .71$). Nevertheless, in good underwater visibility conditions, all focal cowtails rested on their own; this is a significant increase over rays traveling in poor underwater visibility, where only three of the 15 focal cowtails settled by themselves ($\chi^2 = 20.0$, $df = 1$, $p < .0001$). Cowtails passed a similar number of cowtails and whiprays (all resting solitary) in good underwater visibility conditions (14 and 13, respectively) and encountered more cowtails than whiprays in poor underwater visibility conditions (29 versus 13). Although cowtails in good underwater visibility traveled greater average distances than in poor conditions (305 versus 203 m), this difference was not significant ($t = 1.12$; $p = .14$).

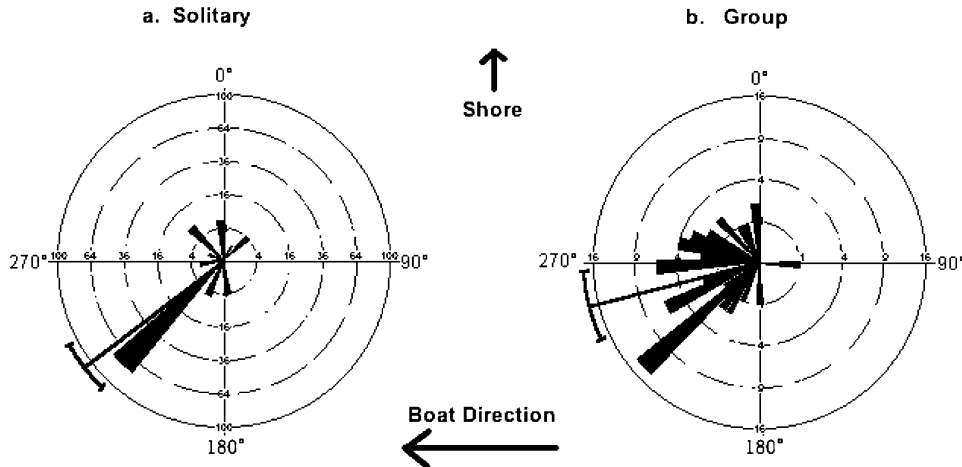


Figure 5

Circular frequency distributions of escape trajectories of (a) solitary cowtail in good underwater visibility and (b) grouped rays (single-species cowtails and mixed species) in poor underwater visibility (see Figure 1 for definitions), in relation to the shoreline (0°) and the boat's path (90°→270°). Concentric circles denote frequencies of 1, 4, 8, 16, 25, 36, and 48 solitary rays (a) and 1, 4, 8, and 16 ray groups (b). Rose diagrams are used to allow a better visualization of the data. T-shaped spoke represents overall mean vector ± 95% confidence limits.

However, cowtails did travel for significantly longer average times before settling in good underwater visibility conditions (opposite of predicted: 12.4 ± 3.7 min versus 8.9 ± 1.9 min; $t = 1.83$; $p = .04$ [one-tailed test]).

DISCUSSION

Results from this study reveal that a cowtail groups significantly more frequently in poor underwater visibility conditions (low VI due to turbidity and/or low incident light levels). Furthermore, in these conditions, its ability to detect predators is affected as a solitary cowtail's response to predators in these conditions is significantly delayed. Grouping is beneficial when underwater visibility is reduced owing to protective spatial arrangement, a significant increase in FID (early warning), and perhaps highly coordinated escape behaviors. However, grouping also has its own costs, including interference in escape between group members and significantly decreased escape speeds of grouped rays compared to solitary.

Effect of environmental variables on flight response

The predator-approach experiment conducted on solitary, resting cowtails demonstrated that FID was positively correlated with VIs and light conditions. Julian date (span of 51 days) was a nonsignificant variable removed from the model ($F_{10,38} = 1.49$, $p = .23$); this implies no habituation to the presence of a model shark in the resting area (and is accordant with the assumption of no pseudoreplication). The results from the experiment are consistent with the hypothesis that a cowtail responds to a predator at the limit of its visual range so as to immediately reduce its predation risk. However, the economic hypothesis of Ydenberg and Dill (1986) states that detection and escape are not necessarily simultaneous. An animal will trade off the benefit of maintaining its current activity with the cost of remaining too long, leaving at the point where it could still successfully escape, with its own visual capability unchanged relative to its predator (Fitzgibbon, 1994; Jarman and Wright, 1993).

We do not believe this explanation applies to our system. While the stingray's visual system possesses adaptations to facilitate predator localization, this system functions optimally in well-lit environments (Gruber et al., 1990; Murphy and Howland, 1990; Perrine, 1999). The cowtail's main predators, various shark species, however, are capable of hunting at night and can detect even buried prey up to 1 m away using electroreception (Haine et al., 2001; Klimley, 1993). Addi-

tionally, video footage of escaping cowtails revealed no obvious detection behaviors before escape, that is no spiracle fluttering (denoting an increase in oxygen consumption), undulations of the pectoral fins, or reorientation of the disc prior to take off. Lastly, fleeing cowtails often demonstrated a lack of awareness of their surroundings in poor underwater visibility conditions, colliding with sunken, wooden fence posts and/or observers. Based on these lines of evidence, we suggest that a cowtail's visual ability is indeed limited in poor underwater visibility conditions, and it is the change in predator-detection ability (and hence the concomitant increase in risk) that both influences FID and is the driving force behind the facultative grouping behavior of cowtails.

Benefits of grouping

Protective spatial arrangement

In poor underwater visibility conditions, the typical group size was approximately three and the spatial positioning consistently rosette, with individuals closely spaced. Circular formations offer an obvious advantage—namely, the increased ability to detect and monitor the approach of a predator from any direction, and this is accomplished by an increase in the sensory range and/or the reduction of blind spots (Kelly et al., 1999). Close neighbors also make better predator-detecting partners (Pöysä, 1994), as information about a predator is easier to obtain from nearby individuals (Roberts, 1996), an important advantage in poor underwater visibility conditions. Furthermore, the choice of shallow resting waters forces predators to approach alongside the cowtails rather than from above, and the rosette pattern therefore ensures that the tail will be the first body part most likely contacted by the predator. Composed of a thin

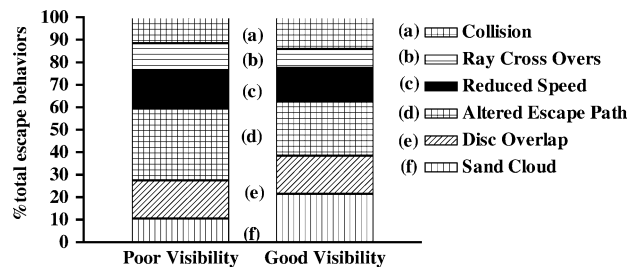


Figure 6

Percentage of each type of interference behavior in poor and good underwater visibility conditions (see Figure 1 for definitions) potentially affecting escape ability in groups (see text for detail).

Table 4
Comparison of escape speeds (meters per 3 s) of different group sizes using an ANCOVA with FID as the covariate

	Solitary ray		Group 2–3		Group 4+		Fastest in group	
	Slope	Speed	Slope	Speed	Slope	Speed	Slope	Speed
Poor visibility ^a	-0.28a (<i>n</i> = 57)	2.34	-0.14b (<i>n</i> = 45)	1.68	-0.16b (<i>n</i> = 7)	1.65	-0.25a (<i>n</i> = 40)	2.04
Good visibility ^a	-0.12a (<i>n</i> = 86)	2.78	-0.16b (<i>n</i> = 22)	1.60				

^a See Table 1 for definition.

Values given are the slope of speed versus FID and the least squared mean speed correcting for FID. The speed of the fastest ray to escape from a group is for a cowtail stingray only. Same letter within VI category: no significant difference. Different letters within VI category: significant difference ($p < .05$).

cartilaginous rod and skin, the tail not only can be sacrificed as a nonessential body part but can also be used to detect predators through the mechanoreceptor system (Maruska and Tricas, 1998; Perrine, 1999). The rosette formation may therefore further enhance a grouped cowtail's chance of detecting a predator by promoting other detection sensory modes when visual ability is limited.

Early warning

With increasing group size, more predator detectors are available with varying abilities that can positively affect reaction distances (Lima, 1995). Because we could not determine the level of vigilance of resting cowtails, we can only speculate about the extent to which levels of vigilance differed as a function of group size. Grouped cowtails responded at greater distances to the approach of a mock predator than did solitary cowtails across a range of VIs: 1.5 times as far in poor underwater visibility conditions (150 versus 100 cm FID, on average) but only 1.17 times further in good underwater visibility conditions (300 versus 256 cm FID). The response-distance advantage of groups over solitaires may mean life or death to a cowtail with limited visual capability but may have little relevance to a cowtail whose visual ability is unimpaired, resulting in the evolution of environmentally contingent grouping behavior in this species.

Concerted escape

While the initial departure of grouped rays did not appear to be coordinated (owing to the variable initial orientation of members, their extraction from the sand, collision avoidance behaviors, and actual collisions), most quickly rejoined one another to flee concertedly from the boat. Such behavior may have the added benefit of confusing the predator because multiple, closely spaced prey make it difficult for a predator to

select a target as individuals become confused with others in the predator's visual field (Curio, 1976; Milinski, 1977). Even though a group of two individuals has been shown to confuse a predator (Hobson, 1978), the confusion effect is effective only if the group remains coherent and the members' movements coordinated. Solitary and grouped cowtails consistently escaped 45° away from the predator (which could maximize distance while keeping the predator at the limits of their visual range; Hall et al., 1986), and group members escaped with very little angular dispersion. Combined together, these two escape behaviors may contribute to the benefit of being in a group if they provide a sensory burden to the predator and make capture more difficult.

Costs of grouping

Interference behaviors

Whereas many vigilant, optimally positioned, closely spaced group members may enhance detection abilities and hence response times, they may also cause a simultaneous decrease in escape ability in other group members (Elgar, 1989; Fitzgibbon, 1990; Hilton et al., 1999; Kenward, 1978). Vigilant group mates that respond immediately to the threat of predation can make slower reacting, nonvigilant members more vulnerable by concealing the predator (via a plume of sand) and its direction of approach (Lima, 1994). Overlapping discs of resting rays, although an effective way to transmit information, can also impede one another's escape. Once they had fled, cowtails occasionally crossed over resting rays, which could have simultaneously switched the focus of a predator, as well as blocked the vision of the resting ray (Bednekoff and Lima, 1998). A cowtail switching escape angles to avoid collision would sometimes cause a noticeable reduction in escape speeds of other rays, and collisions

Table 5
Focal follow data listing mean underwater VI (cm), the number of focal cowtails that rested on their own, the mean number of rays passed before the focal cowtail settled, their mean distance (cm) from the focal ray's path, the mean total distance traveled (m), and the time taken (min) to do so

	Poor visibility ^a (<i>n</i> = 15 rays)	Good visibility ^a (<i>n</i> = 15 rays)	Test statistic	<i>p</i> value
VI (cm) ± 95% CI	162.7 ± 12.3	228.0 ± 5.6	10.37	<.001 ^b
Number of focal rays resting on own	3	15	20.00	<.001 ^c
Mean number of passed rays ^d ± CI (range)	2 ± 1.0 (0–6)	1.8 ± 0.43 (1–3)	0.38	.71 ^b
Mean proximity to passed ray (cm) ± CI (mode)	50.2 ± 12.2 (75)	55.9 ± 8.9 (75)	0.64	.52 ^b
Mean distance traveled (m) ± CI (range)	203.3 ± 147.0 (50–1000)	305.3 ± 129.8 (40–750)	1.12	.14 ^b
Mean time traveled (min) ± CI (range)	8.9 ± 1.9 (5–15)	12.4 ± 3.67 (5–28)	1.83	.04 ^b

^a Unpaired *t* test.

^b Chi-square test.

^c See Table 1 for definition.

^d A group was counted as a single pass.

between two or more escaping cowtails occurred with moderate frequency. These behaviors, all occurring immediately post-flight initiation, may be responsible for reducing the average escape speed of a group compared to a solitary cowtail, for keeping group sizes small, and possibly for maintaining facultative grouping in this species.

Large groups were rare, supporting the hypothesis that grouping is costly. Typical group sizes ranged from 2.3 to 2.8 depending on environmental conditions, with the largest observed group size being nine ($n = 1$ group). Cowtail group size may be limited by the costs of increased conspicuousness, an increased rate of dermal ectoparasite transmission (Chisholm et al., 2001; Semeniuk, personal observation), and increased escape costs. Escape costs would increase with increasing group size to a point where the predator could potentially be on the last member to leave a group before it had a chance to flee (Lima, 1994).

Decreased escape speeds

The speeds at which cowtails escaped from an approaching boat were dependent on the distance at which they initiated flight (i.e., the closer the boat, the higher the speeds). Controlling for flight distance, solitary cowtails escaped at significantly higher speeds than those in groups, regardless of visibility conditions. The decreased mean escape speed of a grouped ray may pose too much of a cost in good underwater visibility conditions when a cowtail has no difficulty in visually detecting a predator and can escape at a safe distance. However, with its visual ability compromised, a cowtail may be willing to join a group for its net antipredator advantages and to experience the costs of having an initially decreased escape speed as its chances of surviving are still greater than when on its own. The escape speed of the fastest cowtail within a group in poor underwater visibility conditions was not significantly different from the speed of a solitary cowtail, suggesting that a grouped individual still perceives the same amount of risk as a solitary and responds accordingly. This implies that additional factors may have prevented all grouped rays from escaping at the same high speed.

Alternative costs to grouping

The alternative hypothesis examined, that cowtails group for non-antipredator reasons only in relatively safe conditions (i.e., poor underwater visibility conditions for the predator), is based on the notion that many animals experience predation when searching for resources or traveling between sites because movement creates strong visual and mechanical stimuli for predators (Kramer and McLaughlin, 2001; Martel and Dill, 1995). It is quite possible, therefore, that a cowtail may experience high predation costs while searching for a suitable resting partner and be reluctant to search for groups in good underwater visibility conditions due to increased conspicuousness. Because cowtails in good underwater visibility conditions traveled for longer periods than those in poor conditions, closely passed two rays on average (within a meter), and still rested on their own, it appears that cowtails do not perceive travel as posing much risk. Costs responsible for maintaining solitary behavior in good underwater visibility condition may therefore originate from the formation of the group itself combined with the absence of obvious benefits of grouping under such conditions.

Conclusion

The interplay between costs and benefits of grouping under differing environmental conditions is driven by differences in perceived predation risk and reflected in the facultative grouping behavior of this species. A solitary cowtail in good

underwater visibility conditions has a high probability of detecting and escaping a predator; therefore, benefits of grouping have less of an impact on survival, whereas grouping costs become significant, that is, the net effect of grouping may be negative in good conditions. Similarly, the benefits of being in a group are greater than the costs in poor underwater visibility conditions, and hence, grouping becomes the preferred choice then.

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