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Experimental confirmation of aggressive mimicry by a coral reef fish

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Abstract A number of potential mimetic relationships between coral reef fishes have been described, but the underlying mechanisms are poorly understood. Similarities in colour between species have often been attributed to aggressive mimicry (where predators resemble models in order to deceive prey), however this has not been tested. The fang blenny, *Plagiotremus rhinorhynchos* is a specialized predator that feeds on tissues of other fishes. Some individuals appear to mimic the harmless cleaner wrasse *Labroides dimidiatus* in order to deceive fish visiting cleaning stations, thereby increasing access to food. In this study, the ecological relationship between the mimic and model was examined at Kimbe Bay (Papua New Guinea) and the hypothesis that colour similarities represent facultative aggressive mimicry was experimentally evaluated. Some juveniles exhibited a striking resemblance to the juvenile colouration of the cleaner wrasse, but only when in close proximity to the wrasse and only when similar in size. As predicted for mimics, *P. rhinorhynchos* co-occurred with *L. dimidiatus*, but was rare relative to the model. Among site comparisons showed that the abundance of mimetic type blennies was positively correlated with the abundance of juvenile cleaner wrasses. Approximately 50% of all *P. rhinorhynchos* were found ≤1 m from the nearest *L. dimidiatus*, a distance significantly shorter than expected if they were not associated. A cleaner wrasse removal experiment was carried out to test whether the colour displayed by the blenny and its foraging success were contingent upon the presence of a model. In all cases, removal of the model prompted a rapid colour change to a general non-mimetic colouration in *P. rhinorhynchos*. Removal of *L. dimidiatus* also resulted in a ~20% reduction in the average foraging success of the blenny compared to controls, supporting the hypothesis that the blenny is a facultative aggressive mimic of the cleaner wrasse.

Keywords Colour change · Facultative mimicry · Foraging success · *Labroides dimidiatus* · *Plagiotremus rhinorhynchos*

Introduction

Mimicry is a dramatic example of convergent evolution and can arise in response to a number of selective mechanisms (Gilbert 1983; Turner 1995; Joron and Mallet 1998). In Batesian mimicry, harmless and palatable species closely resemble unpalatable or venomous species usually avoided by predators (Bates 1862). In Müllerian mimicry, two or more unpalatable species share similar colour patterns and thus reinforce their predator deterrence (Müller 1879). Social mimicry arises when species adopt the colouration of another species in order to escape the attention of predators (Moynihan 1968). Conversely, in aggressive mimicry, a predatory species resembles a harmless species in order to deceive potential prey, thus increasing their access to food (Wickler 1965, 1968; Malcolm 1990). Although colour similarities between species can be striking, and might be indicative of mimetic relationships, observations on colour alone are insufficient to confirm mimic-model relationships or to indicate which type of mimicry is involved.

Colour similarities can be potentially explained by mimicry if a number of criteria can be applied (Snyder 1999). Mimetic species must be rare compared to their model species; otherwise the signal receiver will encounter too many mimics and learn from these experiences (Bates 1862). However, an increase in the abundance of models should allow for a corresponding increase in the abundance of mimics. Mimics and models should be of similar body size (Moyer 1977), should co-occur in the same habitat (Randall and Randall 1960) and should have overlapping geographic ranges (Thresher 1978). While

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mimicry can be rejected if a proposed mimic does not meet these criteria, these criteria by themselves are not diagnostic of mimicry. Some species are facultative mimics and only adopt model colouration when in close proximity to a model (Ormond 1980). In these cases, experimental manipulations can provide an unequivocal demonstration of mimicry, if mimics adopt model colouration when they are placed together or lose model colouration when they are separated.

Coral reef fishes are widely appreciated for the dramatic differences in body colour among species (DeMartini and Donaldson 1996; Randall et al. 1997; Marshall 2000). However, distantly related pairs of species exhibiting striking similarities in colour are relatively common, suggesting that mimicry might have been important in the evolution of this group (Wickler 1965; Russell et al. 1976; Thresher 1978). The literature on colour mimicry in reef fishes is largely restricted to descriptions of colour similarity and ad hoc explanations of this phenomenon (e.g. Randall and Randall 1960; Losey 1972; Russell et al. 1976; Moyer 1977; Ormond 1980; Siegel and Adamson 1983). Few studies have established experimentally that colour similarities represent mimic-model relationships and even fewer have been able to establish which kind of mimicry is involved (but see Caley and Schluter 2003).

Aggressive mimicry is the most common form of mimicry postulated for coral reef fishes, with over 30 presumed examples (e.g. Randall and Randall 1960; Wickler 1968; Springer and Smith-Vaniz 1972; Russell et al. 1976; Moyer 1977; Thresher 1978; Ormond 1980; Snyder 1999; Sazima 2002a; Munday et al. 2003) encompassing nine reef fish families. Although in each case aggressive mimicry is a plausible explanation, to date it has not been confirmed by experiments. To establish that a mimetic relationship is a case of aggressive mimicry it must be established that a mimic gains a foraging advantage in the presence of a model, or a reduction in foraging success where a model has been experimentally removed.

In this study, we used a combination of field observations and a manipulative experiment to investigate the basis of mimicry of the cleaner wrasse *Labroides dimidiatus* by the blenny *Plagiotremus rhinorhynchos*. Members of the genus *Plagiotremus* are obligate feeders on mucus, dermal tissue and scales from the body surface of fish (Wickler 1961; Hobson 1969; Springer and Smith-Vaniz 1972; Russell et al. 1976; Smith-Vaniz 1976; Kuwamura 1983; Randall et al. 1997). The Indo-Pacific species, *P. rhinorhynchos*, is known to display a range of colour phases (Smith-Vaniz 1976; Randall et al. 1997), with the blue phase proposed to be an aggressive mimic of the cleaner wrasse, *L. dimidiatus* (Wickler 1961; Russell 1976; Russell et al. 1976; Kuwamura 1981, 1983; Randall et al. 1997). *P. rhinorhynchos* is thought to benefit from mimicking *L. dimidiatus* by feeding directly on fishes that are attracted to the cleaning stations. *P. rhinorhynchos* also exhibits an orange phase that is thought to be an aggressive mimic of *Pseudanthias squammipinnis* (Russell et al. 1976; Randall et al. 1997). However, whether these colour similarities represent true mimicry, and if so, which type of mimicry, have not been investigated. The juvenile colouration of *L. dimidiatus* is very distinctive (Mahon 1994) and the resemblance between *L. dimidiatus* and *P. rhinorhynchos* is considered to be most striking between juveniles of the two species (Russell 1976; Russell et al. 1976; Kuwamura 1981).

To establish whether the similarity between juvenile *P. rhinorhynchos* and juvenile *L. dimidiatus* is a case of mimicry we tested the following predictions: (1) mimics and models should co-occur within the same habitat and the abundance of the mimic should be substantially lower than that of the model, (2) the abundance of the mimic should increase in response to increase in model abundance and (3) the body size range of mimics should

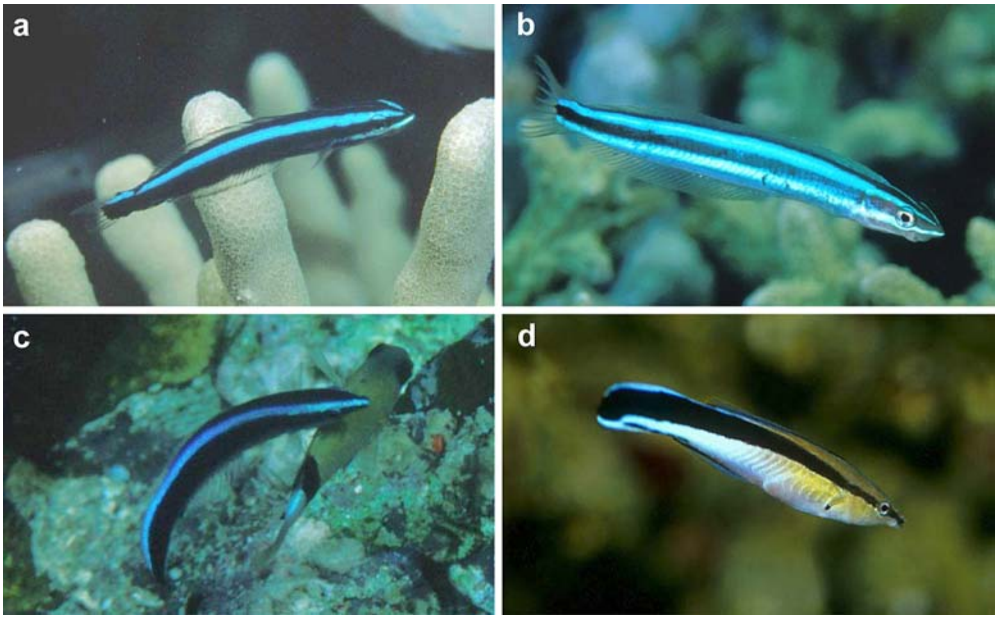

Fig. 1a–d Different colour phases of *P. rhinorhynchos* and *L. dimidiatus*. **a** Mimetic juvenile *P. rhinorhynchos* (4 cm TL). **b** Non-mimetic adult *P. rhinorhynchos* (7.5 cm TL). **c** Juvenile *L. dimidiatus* (4 cm TL). **d** Adult *L. dimidiatus*. Photo of adult *L. dimidiatus* courtesy of J Jensen (http://www.jjphoto.dk). All other photos by E. Moland

conform to the body size range of models. If aggressive mimicry is responsible for the similarity in colouration between *P. rhinorhynchos* and *L. dimidiatus*, we also predicted that (4) individuals exhibiting mimetic colouration would be in close proximity to individuals of *L. dimidiatus*, (5) mimics would lose model colouration following experimental removal of model individuals, and (6) the foraging success of mimetic *P. rhinorhynchos* individuals would decrease following removal of the model.

Materials and methods

The location and species

This study was conducted at Kimbe Bay on the island of New Britain, Papua New Guinea (5°15′S 150°15′E) during August 2003. Observations on the distribution, abundance and dispersion of *P. rhinorhynchos* (mimic) and *L. dimidiatus* (model) were made on ten different emergent reefs ranging between 1 and 5 km offshore, separated by expanses of water in excess of 100 m deep. The model removal experiment was carried out on two of these reefs along the southern shores of Schaumann (Garalla) and Restorff (Kaula) Islands.

Each *P. rhinorhynchos* encountered was classified as a mimetic (Fig. 1a) or non-mimetic (Fig. 1b) colour phase. Mimetic colour phases were characterised by an all over black colouration with the upper electric-blue lateral stripe and only the very anterior part of the lower lateral stripe visible. Non-mimetic colour phases were characterised by possessing a complete lower as well as an upper lateral stripe and varying body colouration. Each *L. dimidiatus* was classified into a life history stage according to its size and colour. Juveniles were recognized by their conspicuous colouration; a black body colour with an electric-blue lateral stripe originating at the mouth and terminating at the upper edge of the caudal fin (Fig. 1c). Adult *L. dimidiatus* have a thin black lateral stripe originating at the mouth that widens towards the posterior end of the body and terminates in a largely black caudal fin (Fig. 1d). Ventral parts of the body are white near the anterior and grade to light blue at the posterior. The dorsal colour is grey to light brown at the anterior, blending to a light blue posterior.

Distribution and abundance of putative mimics and models

The distribution and abundance patterns of *P. rhinorhynchos* and *L. dimidiatus* were estimated using visual census, to test the predictions that mimics should be rare relative to models, and the abundance of mimics should be positively related to the abundance of models. At each of the ten reefs we surveyed three 6×50 m transects running parallel to the reef crest, with the mid-line of each transect positioned at 3–5 m depth. Transects were laid out haphazardly, with at least 10 m between consecutive transects. The size and position (coordinates) of individuals of both species within transects were recorded on data sheets drawn to scale. The potential among-site relationship between the abundance of juvenile *L. dimidiatus* models and that of mimetic *P. rhinorhynchos* colour phases was examined by linear regression.

Body size relationships between mimics and models

Total length was estimated for all *P. rhinorhynchos* and *L. dimidiatus* observed, to test the prediction that mimics should only adopt model colouration when they overlap in body size. The frequency distributions of total length estimates for mimetic and non-mimetic *P. rhinorhynchos* were compared to those of juvenile and adult *L. dimidiatus* in order to examine whether the putative *P. rhinorhynchos* mimics are more prevalent in the smaller size classes and associated with sizes of juvenile *L. dimidiatus*.

Behavioural association between mimics and models

The potential relationship between the dispersion of *P. rhinorhynchos* and that of *L. dimidiatus* was examined in order to test the prediction for aggressive mimicry, that mimics should be closely associated with the model. The distance from each mimic or non-mimic blenny to the nearest cleaner wrasse was measured within each transect using the co-ordinates recorded for all individuals along each transect. To determine whether mimics and non-mimics were in closer proximity to models than would be expected by chance, the mean distance between blennies and cleaner wrasses was compared to the mean distance between blennies and random co-ordinates placed on each transect. The difference in distance to nearest *L. dimidiatus* between mimetic and non-mimetic *P. rhinorhynchos* colour phases was compared using a two-tailed *t*-test.

The use of space by ten mimetic *P. rhinorhynchos* associated with a juvenile *L. dimidiatus* model was examined to assess the degree of association between the putative mimics and models, and to test the following specific predictions about the association: (1) mimics and models should have bordering or overlapping home ranges if the proposed mimic-model relationship involves a spatially and temporally stable association, (2) as the beneficial cleaning behaviour exhibited by *L. dimidiatus* is the underlying ecological basis for the proposed mimicry, the juvenile cleaner models should allocate a substantial amount of their time to this behaviour, and (3) if the presence of a model is advantageous to the foraging of the mimic, then at least some of its foraging should occur in immediate proximity to the model.

All of the ten mimic-model pairs were more than 30 m apart and separated by the home range of at least one non-mimetic *P. rhinorhynchos*. The location of the mimic-model pairs ranged in depth from 3 to 9 m and each was marked with a numbered subsurface buoy. The mimic-model pairs were sampled randomly across time of day and tides over 2 consecutive days.

Each mimic *P. rhinorhynchos* was observed for 30 min during which the following variables were recorded: (1) The frequency of successful feeding strikes: a successful strike was defined as physical contact between mimic and a target prey individual sufficient to cause a jolt in the "prey" fish. (2) The frequency of unsuccessful strikes: An unsuccessful strike was noted when a mimic appeared to abort an attack or did not make contact with the "prey" fish. The proximity of the model when feeding strikes occurred was recorded as either >1 or ≤1 m from the model. The size of all target "prey" fish was recorded. The behaviour and location of the ten juvenile *L. dimidiatus* models was recorded every 30 s for 15 min in order to establish the time allocated to cleaning. The behaviours exhibited by the model were grouped into the five categories: cleaning, displaying, travelling, sheltering and other activities.

The home ranges of mimic *P. rhinorhynchos* and nearest juvenile *L. dimidiatus* were examined to calculate overlap in daily movements. Positions on the substratum were marked off simultaneously during the 30-min sampling time for mimics, and during the 15-min sampling time for models by dropping numbered tags. Measurements among tags were then made to produce a scale drawing of the home range. Home ranges were measured using Microsoft Image Tool according to the maximum-area polygon method (Sanderson 1966). Mean home range sizes were calculated for the ten mimics and models. Percentage home range overlap was calculated for each mimic-model pair. A two-tailed paired sample *t*-test was used to compare the home range sizes for mimics and models.

Model removal experiment

We conducted a model removal experiment in order to test the following two predictions: (1) if mimicry of *L. dimidiatus* was facultative, mimics would lose model colouration following experimental removal of models, (2) based on the proposed foraging benefit of aggressive mimicry foraging success of mimetic *P. rhinorhynchos* colour phases would decrease following removal of the model. It was not possible to relocate juvenile *L. dimidiatus* in the field, so a reciprocal addition treatment was not possible.

The ten mimic-model pairs previously studied were haphazardly divided into five control and five treatment pairs. Photographs were taken of each mimic and model individual prior to the model removal in order to document initial colouration. The juvenile *L. dimidiatus* in the five treatment pairs were then captured using a fence net and clove oil, and relocated to a reef 10 km away from the experimental sites.

The five treatment and five control mimics were sampled 1 day after and 7 days after model removal, photographing each individual to examine colour change and making behavioural observations to examine foraging success (number of successful and unsuccessful strikes in 30 min as above). Home ranges were also measured to determine whether model removal resulted in any changes in the shape, size or position of mimic home ranges. All treatment and control sites were sampled randomly across time of day and tides.

Foraging data were converted to percent successful strikes. Means for treatment and control were calculated for 'before', 'day 1' and 'day 7' data. Differences between control and treatment were compared using two tailed paired sample *t*-tests. As recommended for proportions, data were arcsine transformed prior to analysis to correct for normality violations at low and high values (Zar 1999). The levels of aggression by prey fish and potential prey fish data was also examined in order to test whether mimics suffered from a greater level of aggression from target fish following the removal of models.

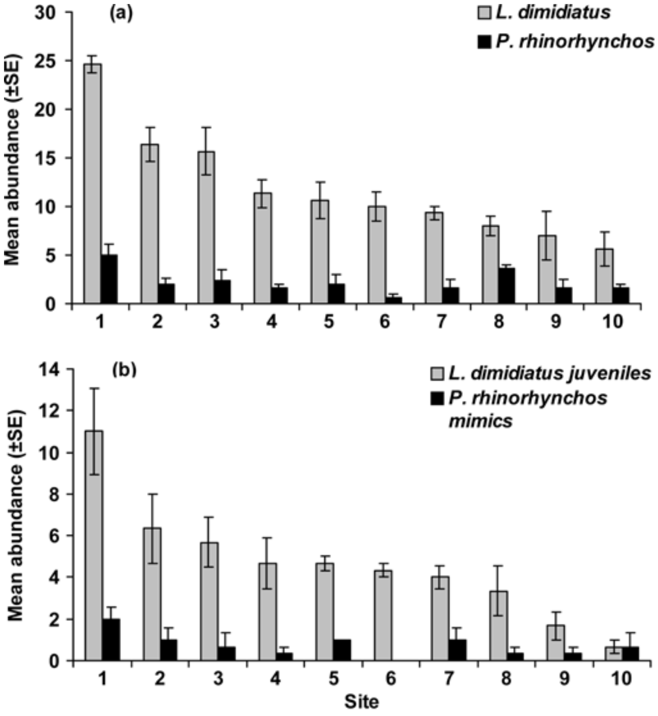

Fig. 2a, b Mean density estimates per 300 m^2 for *L. dimidiatus* and *P. rhinorhynchos* at ten sites in Kimbe Bay, Papua New Guinea. **a** Abundance of all life history stages of *L. dimidiatus* and all colour phases of *P. rhinorhynchos*. **b** Abundance of juvenile *L. dimidiatus* and mimetic *P. rhinorhynchos* colour morphs at the same ten sites. *Error bars* standard errors. Sites are ranked from the highest to lowest in abundance of *L. dimidiatus*

Results

Abundance and distribution

Both *L. dimidiatus* and *P. rhinorhynchos* co-occurred at all ten reefs sampled in Kimbe Bay (Fig. 2a). However, the average abundance of *L. dimidiatus* (juveniles and adults combined) varied considerably among sites, ranging from 6 to 25 individuals, while the average abundance of all *P. rhinorhynchos* (mimics and non-mimics) varied from 1 to 5 fish per site. The abundance of *P. rhinorhynchos* was consistently lower than that of *L. dimidiatus* (on average 19%), although this varied from 7 to 45%. Furthermore, there was a significant correlation between the total numbers of *L. dimidiatus* and *P. rhinorhynchos* within and among sites (OLS regression: $F_{1,8}$=5.787, P<0.05, r^2=0.44).

Nearly 20% of all *P. rhinorhynchos* were found to exhibit distinct mimetic colouration. Juvenile *L. dimidiatus* and mimetic *P. rhinorhynchos* colour phases co-occurred at nine out of ten reefs sampled (Fig. 2b). The average abundance of juvenile *L. dimidiatus* varied considerably among sites, ranging from 1 to 11 individuals, while the average abundance of mimetic *P. rhinorhynchos* varied from 0 to 2 fish per site. The abundance of mimetic *P. rhinorhynchos* was usually lower than that of juvenile *L. dimidiatus* (on average 23%). There was a significant relationship between the numbers of juvenile *L. dimidiatus* and mimetic *P. rhinorhynchos* among sites (OLS regression: $F_{1,8}$=9.432, P<0.05, r^2=0.55).

Body size relationships between mimics and models

Mimetic colour phases were more prevalent in the smaller size classes of *P. rhinorhynchos* than in large size classes. The mean size (TL) of mimics was 5.04 cm ± 1.04 SE, compared with 5.87 cm ± 0.80 SE for non-mimetic colour phases. The largest mimic observed was 6 cm (TL). Mimics were not the most prevalent colour phases in any size class, with many small fish observed that were non-mimetic (Fig. 3a). Importantly, the size distribution of mimetic *P. rhinorhynchos* coincided with the size distribution of the largest *L. dimidiatus* juveniles (Fig. 3b). The mean size of mimics was 5.15 cm (TL) ± 0.15 (SE), which was slightly larger than the mean size of models (4.00 ±0.22). The size that mimetic *P. rhinorhynchos* colour phase declined corresponded with the ontogenetic shift in colouration of *L. dimidiatus* (Fig. 3a, b).

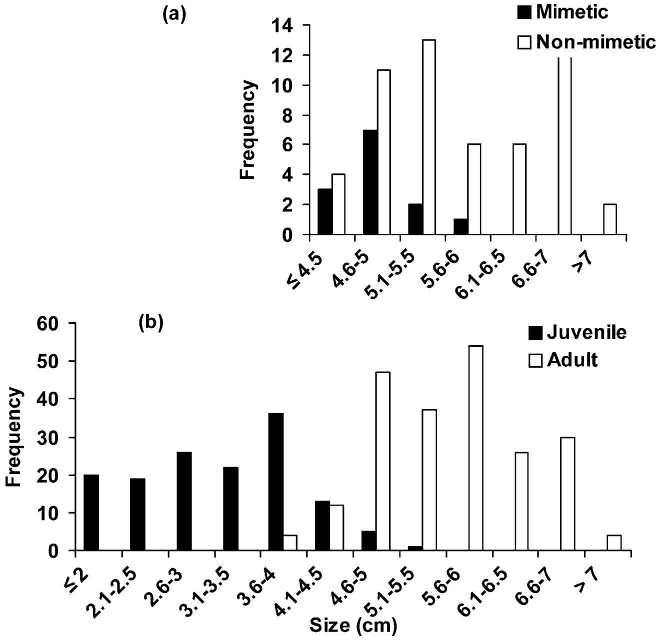

Fig. 3a, b Comparison of body size (total length) frequency distributions for **a** mimetic and non-mimetic forms of *P. rhinorhynchos*, and **b** juvenile and adult forms of *L. dimidiatus* for ten sites surveyed at Kimbe Bay, Papua New Guinea. Sample sizes were: mimetic *P. rhinorhynchos* (n=13), non-mimetic *P. rhinorhynchos* (n=54), juvenile *L. dimidiatus* (n=142), and adult *L. dimidiatus* (n=214)

Dispersion and association

The vast majority of *P. rhinorhynchos* were found less than 1 m from an individual of *L. dimidiatus*. The average distance from all *P. rhinorhynchos* (n=67) to the nearest *L. dimidiatus* was 1.90 m ± 0.27 (SE), which contrasted with an average distance from all randomised position co-ordinates (n=67) to the nearest *L. dimidiatus*, which was 3.91 m ± 0.42 (t-test: t=4.02, df=66, P<0.05). Approximately 50% of all *P. rhinorhynchos* (n=32) were within the ≤1 m of a *L. dimidiatus*.

Ninety two percent of mimetic *P. rhinorhynchos* colour phases were closely associated with a juvenile *L. dimidiatus*. The average distance from mimetic *P. rhinorhynchos* colour phases (n=13) to the nearest *L. dimidiatus* was 1.73 m ± 0.48 (SE), which was not significantly different from the average distance from non-mimetic *P. rhinorhynchos* colour phases (n=54) to the nearest *L. dimidiatus* was 1.94 m ± 0.26 (t-test: t=0.36, P<0.05).

Behavioural interactions between mimic and model

The mean home range size for mimics was 25.23 m^2± 7.98 (SE), which was not significantly different from the mean home range size for models (15.08 m^2 ± 4.78). There was also no significant difference between home range sizes of mimetic *P. rhinorhynchos* and associated juvenile *L. dimidiatus* in the ten mimic-model pairs studied. The average home range overlap between mimics and models was 60%, although home range overlap ranged from 6% (a smaller model home range embedded in a larger mimic home range) to 100% (a smaller mimic home range embedded in a larger model home range).

Juvenile *L. dimidiatus* spent on average 34% of their time on cleaning behaviour, their most common activity. Time spent on this behaviour varied from 20 to 53% among the 10 individuals surveyed.

Eighty percent of strikes observed in the ten mimetic *P. rhinorhynchos* colour morphs were successful in biting a "prey" fish. All strikes within a distance ≤1 m from the model were successful.

Model removal experiment: colour change and foraging success

All *P. rhinorhynchos* in the ten mimic-model pairs studied displayed the mimetic colouration prior to the model removal experiment (Fig. 4a). We observed colour change in all five mimics that had their model individuals removed. Colour change began on the same day the model was removed and was complete 7 days later. On day 1, the lower lateral stripe characteristic for non-mimetic *P. rhinorhynchos* had appeared and the previously black body colouration had become dark reddish brown (Fig. 4b). The black colour was retained on the caudal peduncle and in an area immediately anterior of the caudal peduncle (Fig. 4b). By day 7, four of five mimics without models were similar in colouration to non-mimetic *P. rhinorhynchos* except for the retention of a black spot on the caudal peduncle (Fig. 4c). The fifth treatment mimic maintained the day 1 colouration throughout the duration of the experiment. No colour change was observed in any of the control mimics.

Foraging success declined for mimics following removal of the models. Mimics underwent a ~10% decline in foraging success (% successful strikes) after 1 day of model removal and a ~20% decline in foraging success after 7 days. Foraging was significantly lower in the treatment mimics than in the controls on day 7 (t-test: t= −4.214, df=4, P<0.05) (Fig. 5a).

The decline in foraging success by treatment mimics appeared to be compensated for by an increase in the total number of attempted strikes (Fig. 5b). The number of total attempted strikes in treatment mimics was significantly higher than that of controls on day 1 (t-test: t=3.203, df=4, P<0.05) and day 7 (t-test: t=4.275, df=4, P<0.05) (Fig. 5b). The mean number of aggressive behaviours from "prey" fishes directed towards the blennies increased dramatically following model removal (day 7, t-test: t=2.851, df=4, P<0.05) (Fig. 5c).

Discussion

Most presumed cases of aggressive mimicry in coral reef fishes represent untested hypotheses based only on

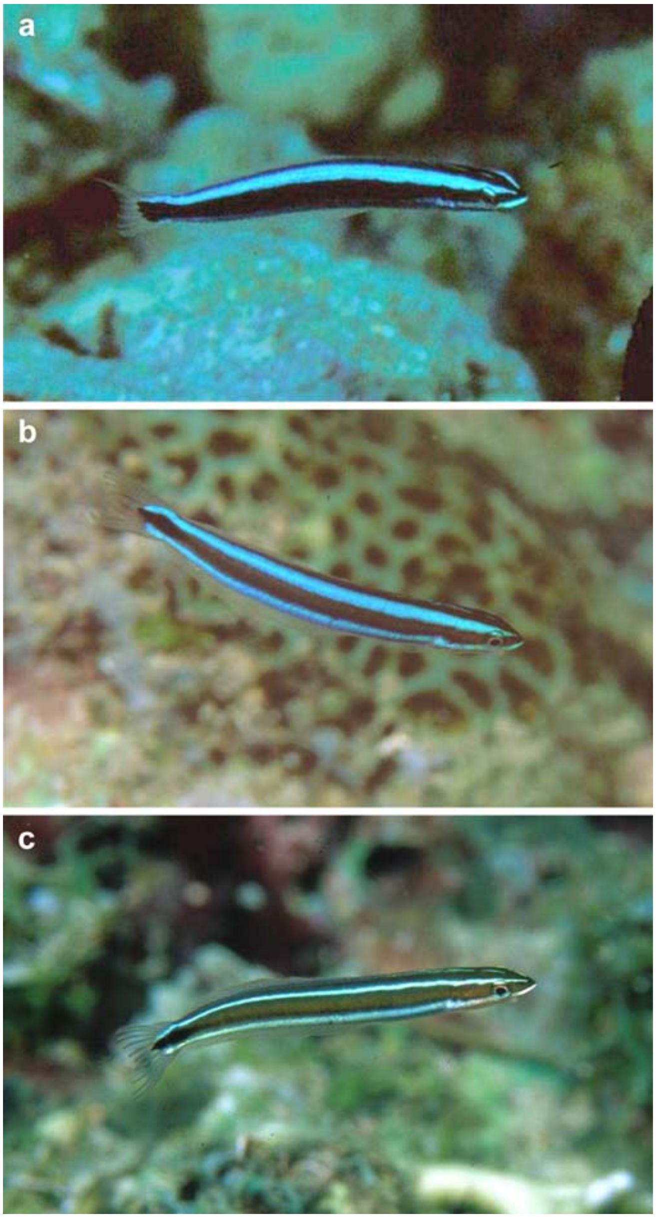

Fig. 4a–c Colour change in a mimic *P. rhinorhynchos* following the removal of its model *L. dimidiatus*. **a** Before removal (mimic colouration). **b** One day after model removal. **c** 7 days after model removal. Note indentation behind operculum. Photos by E. Moland

descriptions of colour similarities. Our study provides strong observational and experimental evidence that convergence in colour between smaller *P. rhinorhynchos* and juvenile *L. dimidiatus* is an example of aggressive mimicry (sensu Wickler 1965). This conclusion supports Russell (1976), who was the first to document the resemblance between juvenile *P. rhinorhynchos* and *L. dimidiatus*, and put forward the hypothesis of aggressive mimicry. Our observations showing the close association between mimics and models, the rapid colour change following model removal and the reduction in foraging success confirms that the resemblance to juvenile *L. dimidiatus* represents aggressive mimicry.

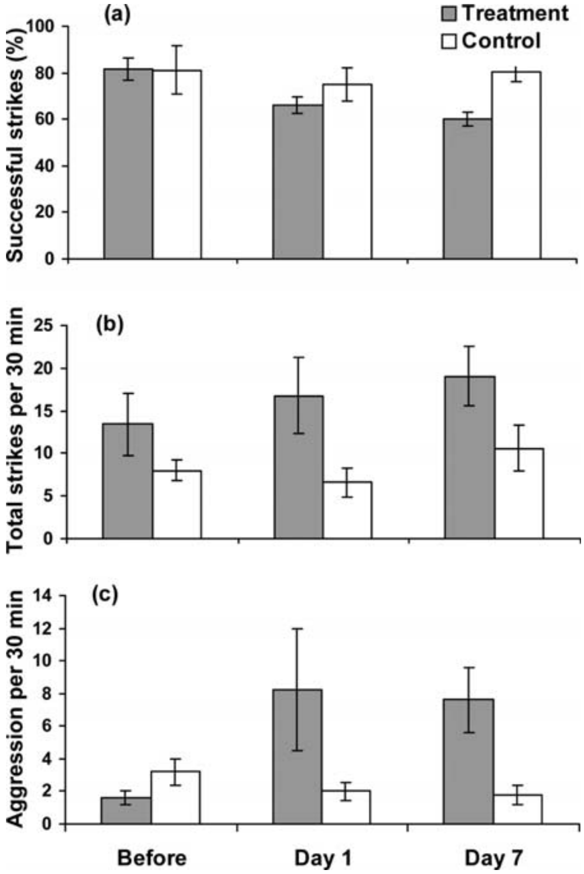

Fig. 5a–c Behavioural responses of *P. rhinorhynchos* to removal *of L. dimidiatus*. **a** Mean percentage foraging success observed in treatment (*n*=5) and control mimics (*n*=5) before model removal, and on day 1 and day 7 after model removal. **b** Mean number of attempted feeding strikes before model removal, and on days 1 and 7 after model removal. **c** Mean number of aggressive attacks by attempted target before model removal, and on day 1 and day 7 after model removal. *Error bars* 95% confidence limits

The mimetic relationship between these two species is facultative and the presence of a model is essential for *P. rhinorhynchos* to adopt mimetic colouration. Smaller *P. rhinorhynchos* appear to be choosing the mimetic colouration in order to maximise their fitness in situations where an opportunity exists to establish a stable association with a juvenile *L. dimidiatus*. The ability to change colour has been described for other mimetic fishes (Wickler 1961, 1968; Losey 1974; Ormond 1980; Kuwamura 1981), although the cues for when to change colour are not always known. Losey (1974) observed colour change in the mimic blenny *Aspidontus taeniatus* from the mimetic colouration to a cryptic colouration (mottled brown and silver white) that it appears to adopt when in pelagic mode. Similarly, Ormond (1980) observed the two labrids, *Cheilinus diagrammus* and *Epibulus insidiator*, temporarily accompany and copy the colour of various model species when foraging.

The close association between *P. rhinorhynchos* and *L. dimidiatus* suggests that mimicry is a significant, although not obligate, aspect of the ecology and behaviour of the mimic. The patterns of distribution and abundance conform to most types of mimicry. The mimic species is rare relative to the model, as observed for many reef fishes (Moyer 1977; Thresher 1978; Bunkley-Williams and Williams 2000; Eagle and Jones 2004). The mimic co-occurs with the model and the abundance of the mimic is positively correlated with the abundance of the model. In this case, *P. rhinorhynchos* remains associated with *L. dimidiatus* long after it has lost mimetic colouration. This suggests that the cleaner plays an important role in determining the patterns in abundance and distribution of *P. rhinorhynchos*. In a similar manner Eagle and Jones (2004) showed that the distribution and abundance of the mimetic juvenile *Acanthurus pyroferus* are promoted by the abundance of the model *Centropyge vroliki*. Mimicry may well play a significant role in maintaining high local species diversity in coral reef communities, as it does in tropical rain forests, by contributing to the persistence of rare mimetic species (Gilbert 1983).

We found a preponderance of *P. rhinorhynchos* displaying the mimetic colouration in the smaller size classes, suggesting that the value of mimicry declines when they out grow juvenile cleaner wrasse. The restriction of mimics to smaller sizes supports observations made at other locations (Russell 1976; Russell et al. 1976; Kuwamura 1981). Although some retain juvenile *L. dimidiatus* colour to a larger size than *L. dimidiatus* do, the transparent caudal fin in *P. rhinorhynchos* makes the blenny look smaller than its actual size from a distance. The transparent caudal fin may in fact be adaptive and allow mimics to prolong the time they can gain from mimetic colouration.

Why is mimicry restricted to the juvenile phase? Apparent mimetic colouration during juvenile stages is extremely common in coral reef fishes (Randall and Randall 1960; Russell et al. 1976; Sazima and Uieda 1980; Dafni and Diamant 1984; Randall and Hoese 1986; Kuiter 1995; Deloach 1999; Snyder 1999; Bunkley-Williams and Williams 2000; Smith-Vaniz et al. 2001; Snyder et al. 2001; Sazima 2002a, b; Eagle and Jones 2004), suggesting that there may be a general explanation. Resemblance to non-related species is possibly more effective during early stages, before species-specific anatomical features become more obvious and the ability to deceive less likely. There may also be greater selective pressure for mimicry at a small size, either because of vulnerability to predators or difficulties in accessing food. Mimics may also simply outgrow their models. Further work is needed to distinguish among these hypotheses.

Mimics were not the most prevalent colour phases in any size class of *P. rhinorhynchos*, with many small fish also not showing mimetic colouration. This raises another question—why are not all juveniles mimics? The simplest explanation would be that there are not enough juvenile cleaners for every juvenile blenny. However, since the abundance of juvenile cleaners far outnumbers the abundance of mimetic blennies, this is not clearly the case. *P. rhinorhynchos* may have a limited ability to locate juvenile *L. dimidiatus* at settlement and may only ‘switch on’ the mimetic colouration when there is one nearby. It should also be noted that we failed to locate any juvenile *P. rhinorhynchos* smaller than 4 cm (TL). Thus we cannot exclude the possibility that the non-mimetic juvenile blennies found had already been through a mimetic phase. The reason for the absence of extremely small mimics is unclear, given that juvenile *L. dimidiatus* were found at much smaller sizes. Either recruitment of *P. rhinorhynchos* was extremely low at the time of the study or it settles at a larger size than the wrasse.

Another question posed by our findings is—why do mimetic juveniles lose mimetic colouration following the loss of their model? Juvenile *P. rhinorhynchos* do not appear to be able to relocate and find other models. Intuitively there is no obvious reason why the blenny should stop being mimetic just because the model has disappeared from its immediate area, because it may still be able to deceive fish that expect to be cleaned. However, it is likely that individuals that never clean will soon be recognized, regardless of their colour. This may explain the increased aggression from “prey” fish following model removal. Cheating behaviour has been documented in *L. dimidiatus*, but host fish stop visiting cleaning stations when cheating becomes too frequent (Bshary and Grutter 2002). Kuwamura (1983) argued that the mimic blenny *A. taeniatus* attacks fish at cleaning stations at a low rate to prevent target fish from learning its disguise. In the total absence of a model, mimic colouration may no longer deceive potential prey and individuals may be more successful adopting adult colouration.

This study has demonstrated that experimental removal of models can be a useful tool for establishing and assessing the ecological benefits of mimicry. There are many other potential cases of mimicry in coral reef fishes, and experimental removal of proposed models will undoubtedly provide new perspectives. Further work on *P. rhinorhynchos*, such as an experimental increase and decrease in model densities, will enable ecological significance of its relationship with *L. dimidiatus* to be more fully assessed. In addition, it is likely that *P. rhinorhynchos* is polychromatic (Russell et al. 1976; Randall et al. 1997), with the ability to approximate the colouration of several fish species or adopt different colours to remain cryptic in different habitats. Transplant experiments could be used to test the ability of individuals to mimic a range of model species and multiple-choice experiments, such as those conducted by Munday et al. (2003), where a putative mimic is given a range of options regarding substratum and alternative models, could be used to determine if some associations were favoured over others.

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