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Sex differences in cleaning behaviour and diet of a Caribbean cleaning goby

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Male and female sharknose cleaning gobies *Elacatinus evelynae* (Gobiidae) occupying cleaning stations in monogamous pairs differed significantly in cleaning behaviour and diet. Females spent five times longer cleaning, took more bites from clients, engaged in more cleaning events on more client species, and cleaned at a higher rate than males. These behavioural differences tended to be reflected in the diet, with more females ingesting more client-gleaned items than males. These results are consistent with greater energetic requirements for reproduction for females. Male cleaning gobies were frequently absent from cleaning stations, presumably guarding eggs, and their presence at cleaning stations gave rise to foraging conflicts and interactions with females. The cleaning rate of females was significantly lowered by the presence of males, whether cleaning or not, whereas males cleaned for longer and took more bites when females were present. When cleaning the same client, males and females showed priority of first inspection, with females cleaning longer and taking more bites in cleaning events they initiated while males gained similar advantages in client- and male-initiated interactions. Furthermore, females initiated cleaning on larger clients, which may give them a foraging priority on a higher-quality resource since larger clients tend to have more ectoparasites. Finally, from a client's perspective, the cleaning service provided appears better in terms of length of inspection and bites taken when both males and females are at a cleaning station than when a single cleaner is present. However, the foraging differences and interactions between male and female cleaning gobies are of little consequence to clients since the cleaning service provided is simply reapportioned between males and females rather than changed by the interactions between gobies.

INTRODUCTION

Cleaner fish involved in interactions during which they remove ectoparasites, mucus and scales from fish clients, display striking differences between species in their propensity to clean, behaviours displayed and specific food items gleaned (review in Côté, 2000). Such differences are also increasingly documented among individuals within species with a concomitant awareness of the potential impacts of this inter-individual variability on cleaner–client relationships. For example, the cleaner wrasse *Labroides dimidiatus* (Valenciennes) ingests significantly more parasites and fewer non-client-gleaned items at Lizard Island than Heron Island on the Great Barrier Reef (Grutter, 1997). The benefits of being cleaned may therefore be more limited at Heron Island, reducing the incentive for clients to visit cleaners. On a smaller scale, Barbadian cleaning gobies *Elacatinus prochilos* (Böhlke & Robins, 1968) occupying coral heads in small groups clean actively and 40% of their diet consists of client-gleaned items, while individuals of the same species living on sponges on the same reef clean only rarely and consume less than 1% client-gleaned material (Whiteman & Côté, in press). The cleaning service offered to clients can therefore differ between cleaning stations within the same reef.

Individual differences in cleaning behaviour, within a cleaner fish species, may result from a range of factors including habitat (e.g. Whiteman & Côté, in press), age and size (e.g. Grutter, 2000). Gender can also be important in determining differences in cleaning. In the only study of sex differences in cleaning behaviour, Arnal & Morand (2001a) found that males and females of the cleaner wrasse *Symphodus melanocercus* (Risso, 1810) differ significantly in behaviour and diet. Females clean more client fish, spend a larger proportion of their time cleaning and consequently ingest a larger proportion of client-gleaned items than males (Arnal & Morand, 2001a). In this species, the sexes occupy discrete territories, or cleaning stations. Individuals therefore engage in cleaning behaviour alone and clients visit the territories of either males or females to be cleaned. In comparison, many cleaning species, particularly in the tropics, occur in pairs or in larger groups on a single cleaning station. For example, *L. dimidiatus* and *L. phthirophagus* (Randall, 1958) can occur in groups of up to five individuals but are most frequently seen in male–female pairs (Feder, 1966). Similarly, cleaning gobies *Elacatinus* spp. in the Caribbean occur singly, in pairs or in groups of up to 40 individuals on a coral head or sponge (Colin, 1975). In such species, cleaning behaviour of individuals might be affected by interactions between males and females on a cleaning station, potentially altering the cleaning service provided to clients across cleaning stations.

We investigated the interactions between males and females of the sharknose goby *Elacatinus evelynae* (Böhlke & Robins, 1968) during cleaning events. *Elacatinus evelynae* are monogamous and paired males and females occupy the same coral head where they both engage in cleaning behaviour (Colin, 1975; Harding, 1994). We compared the

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behaviours of males and females when cleaning alone and accompanied by a partner and considered how interactions between paired individuals affect both the gains from cleaning received by the gobies and the cleaning service provided to client fish.

MATERIALS AND METHODS

Field site and study species

The study was carried out in Barbados (13°10′N 59°30′W), West Indies, between February and October 2000. All observations were made on the north and south sections of the Bellairs Reef in the Barbados Marine Reserve, a 2.2 km stretch of coast containing fringing reefs, on the west coast of the island. Depth on the study site varied between 4 and 9 metres.

We focused on one of the two species of cleaning goby found on the Bellairs Reef. *Elacatinus evelynae*, or sharknose goby, is found singly and in male–female pairs on coral heads (Colin, 1975). Pairs spawn regularly although no synchronicity of spawning has been reported (Harding, 1994). Females produce demersal adhesive eggs which are attached to the roof of a small cavity within a coral head or the reef itself. Following spawning the male tends and guards the eggs alone until hatching, usually 5–6 days later (Thresher, 1984). *Elacatinus evelynae* are sexually monomorphic in terms of coloration and gross morphology. However, sexes can be distinguished by examining the shape of the urogenital papilla. The urogenital papilla of males is long and conical while that of females is short, truncated and often lobed (Thresher, 1984; E.A.W., personal observations).

Eight cleaning stations were identified, each occupied by an adult male–female pair. Cleaning stations were located on four different substrata: the corals *Siderastrea siderea* (Ellis & Solander, 1786), *Montastrea cavernosa* (Linnaeus, 1758), *M. annularis* (Ellis & Solander, 1786) and coralline rock, and all were at the coral–sand ecotone on the edge of the main reef or a patch reef. Distance from shore ranged from 85 to 210 metres. No cleaning stations were located within damselfish territories which can affect the frequency at which stations are visited by clients (Arnal & Côté, 1998) although three stations were adjacent to a longfin damselfish (*Stegastes diencaeus* Jordan & Rutter, 1897) territory.

Individuals were initially identified in one of two ways: by natural distinguishing marks or by marking one goby within a pair using an injection of fluorescent elastomer (VIE, Northwest Marine Technology). Fish were caught in hand nets using clove oil and a single tag was injected into the dorsal tissue close to the tail fin using a 1.5-ml syringe. Fish recovered from the effects of the clove oil within two min and there were no obvious effects of capture or marking. However, to test for impacts of the marking procedure or the mark itself on cleaning behaviour, seven fish were observed five times each for 30 min before and after a tag was injected. There were no significant differences before and after tagging in cleaning behaviour. Three of these test fish each occupied a cleaning station with another goby and the data from these three pairs were added to the cleaning stations observed subsequently for a total of 11 stations.

Individuals were also recognizable on the basis of behavioural differences. Males and females were often located repeatedly in specific locations on the cleaning station. Males were often observed entering and leaving a specific cavity in the coral or reef rock which was assumed to be the nest site. Females were never observed entering the coral cavity.

Observations of cleaning stations

Observations were carried out between 0830 and 1630 hours encompassing the hours during which *E. evelynae* are most active (Johnson & Ruben, 1988; Arnal & Côté, 1998). Each cleaning station was observed 12 times for 30 min, giving a total of 81 hours of observation. Three observations were made at each of four time periods through the day: 0830–1030, 1030–1230, 1230–1430, 1430–1630. Observations were spread throughout the study period; however, all observations for a single cleaning station were completed between 8–60 days.

All cleaning interactions within each observation period were recorded. For each cleaning interaction the identity of the individual initiating the cleaning event (client, female goby or male goby) was recorded. Clients were deemed to initiate a cleaning event by approaching a cleaning station and performing a stereotypical initiation pose, whereas gobies initiated cleaning by swimming from the coral towards a client without prior client posing. The species of each client and whether it was an adult or juvenile, were noted. The length of a cleaning bout, defined as the number of seconds a goby spent inspecting a client, and the number of bites taken which caused the client to flinch perceptibly were recorded for each goby. In addition, the total time a client was inspected, the first goby to start cleaning and the sequence in which the gobies were seen inspecting the client were noted. Finally, a new cleaning event was defined after a goby had spent more than two seconds either resting on the coral surface or swimming in midwater. Cleaning events therefore sometimes involved more than one client individual if the goby swam directly from one client to another.

For all observations at least one goby was present at each cleaning station. Cleaning stations were almost always observed with the female present. The length of time the male goby was present was recorded as well as the number of times the male was seen to disappear and reappear from a cavity in the coral.

Diet analysis

Twenty *E. evelynae* were collected between May and August 2000 (N=14) and June to September 2001 (N=6) using an overdose of clove oil. Cleaning stations were located on *Siderastrea siderea* (7 individuals), *M. cavernosa* (1), *M. annularis* (1), *Agaricia agaricites* (Linnaeus, 1758) (3) and coralline rock (2). Collections were made between 0930 and 1645. Fish were preserved whole in 75% alcohol immediately after the dive. The total and standard length of each fish was measured to the nearest mm and the fish were weighed to the nearest milligram. Sex was assessed externally and confirmed by examination of the gonads.

The entire gut was dissected and split into two sections: the stomach and the intestine. The contents of each were analysed separately. Gut contents were categorized following Grutter (1997) & Arnal & Côté (2000) as: gnathiid isopod larvae, parasitic copepods, free living copepods, fish scales, coral polyps, sponge spicules and tissue and other digested matter. Three methods were used to assess the contents of the stomach and intestine to give measures of both bulk and frequency of each food category (Hyslop, 1980). First, the percentage cover of each food category was estimated. The contents of a 20-mm diameter sampling tray were stirred and then the number of 1 mm^2 squares on the bottom grid covered by each category were counted giving an estimate of the total gut content and the proportion of each food category. Second, individual items of food were counted. Finally, the occurrence of each food item was defined as the number of fish in the sample containing that item (frequency of occurrence).

Data analysis

There was no effect of time of day on the number of clients or species visiting a cleaning station per 30 min, on the total time spent cleaning and the total bites taken per 30 min or on the cleaning rate of individual gobies (Kruskal–Wallis: $P>0.05$ in all cases). Therefore, the data for each observation period were combined in the following analyses.

Data on cleaning interactions were split into four categories for each station. First, all cleaning events were analysed. Differences in the number of clients and species inspected, time spent cleaning, total bites taken on clients and the cleaning rates (bites per second spent inspecting) of males and females were compared. In addition, the cleaning behaviour of females was compared between cleaning events in which she was alone at the cleaning station and those where the male was present, irrespective of whether the male engaged in cleaning behaviour. Second, cleaning events in which both individuals were present at the cleaning station but did not necessarily inspect together were considered. For these cleaning events, the effect in terms of time spent cleaning, bites taken and cleaning rate, on each sex, of cleaning alone while their partner rests on the coral head vs cleaning the same client fish together were compared. Third, cleaning events in which both individuals in a pair inspected the same client or group of clients were analysed. The time spent cleaning, number of bites taken on clients and cleaning rates of males and females were compared according to whether cleaning events were initiated by the male, female, both gobies or client fish (Table 1). Finally, cleaning interactions were considered from the perspective of client fish. Cleaning interactions were compared for clients visiting cleaning stations at which one or both gobies were present and at which one or both gobies engaged in cleaning.

The proportion of events initiated by females, males and clients was also compared for each species of client fish visiting cleaning stations more than five times. Client lengths were estimated as the median length from the range reported by Humann (1989). In addition, to assess the willingness of each goby to clean potentially dangerous vs safe clients, client species were assigned to one of five trophic types based on their diet: planktivore, herbivore, benthic invertebrate predator, omnivore and piscivore (Sale, 1991; Böhlke & Chaplin, 1993). Again, individual cleaning stations were included in the analysis if more than five individuals from a given trophic type were inspected. The number of cleaning stations contributing to the analysis of each client type is therefore variable.

RESULTS

Observations of cleaning interactions

A total of 34 client species belonging to 16 families were observed visiting the focal cleaning stations. We recorded 996 cleaning events during which 1248 clients were cleaned. Excluding brown chromis (*Chromis multilineata* Guichenot, 1853), 99% of all visitors to cleaning stations were cleaned. Brown chromis often visited cleaning stations in schools and gobies cleaned the same individuals repeatedly making it difficult to determine the overall proportion of individuals cleaned. No cleaning events were interrupted by damselfish occupying territories adjacent to cleaning stations. However, both male and female cleaning gobies were observed to chase intruding adult and juvenile *Elacatinus evelynae* and *E. prochilos* from their cleaning station, frequently interrupting a cleaning bout to chase away these intruders.

Males were observed at their respective cleaning stations for 23–99% of the total observation time at each station while females were present 100% of the time,

Table 1. *Proportion of cleaning interactions at all cleaning stations, partitioned according to whether the resident male and female cleaning gobies are present at the cleaning station and which gobies are involved in each cleaning interaction (means ±SD calculated from the average proportion for each cleaning station).*

	% of total interactions		% of interactions
All cleaning interactions	100	Female alone at cleaning station	29.5 ±21.4
		Male alone at cleaning station	3.9 ±7.8
		Both gobies present at cleaning station	66.0 ±21.3
Both gobies present at cleaning station	66.0 ±21.3	Female cleaning alone	46.4 ±18.6
		Male cleaning alone	21.8 ±13.0
		Male and female cleaning	32.8 ±19.0
Both gobies cleaning together	18.8 ±9.7		

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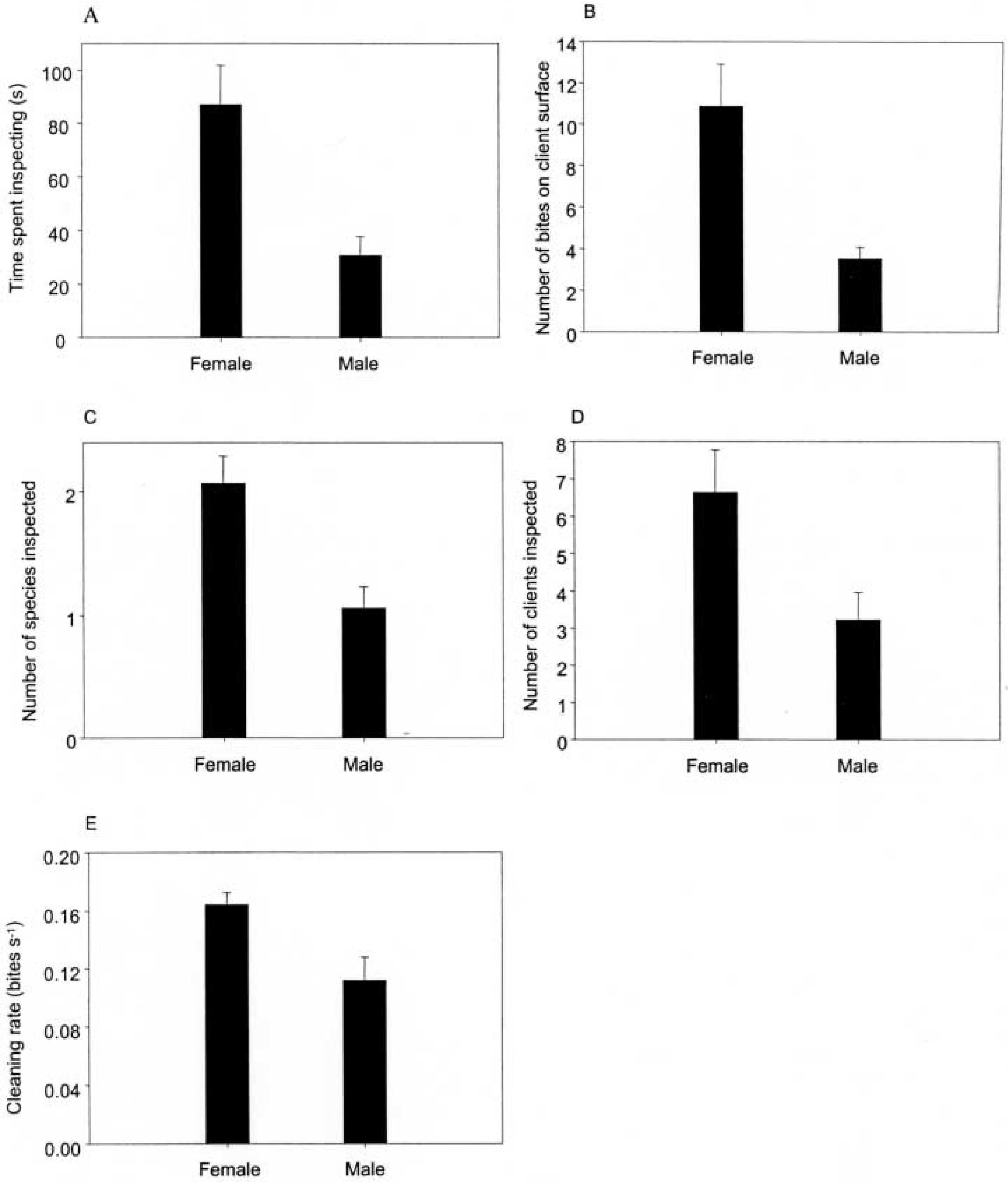

Figure 1. (A) Mean (±SE) time spent inspecting per 30 min; (B) number of bites per 30 min; (C) number of species inspected per 30 min; (D) number of clients inspected per 30 min and (E) cleaning rate per 30 min, for male and female cleaning gobies (N=11 cleaning stations).

except at two sites at which the female was absent for one observation period each. Consequently, on average, females spent 5.14% of their time cleaning as opposed to 1.71% for males. When both gobies were present at their cleaning station females were involved in more cleaning interactions than males (Table 1).

All cleaning events

Females spent significantly more time (Paired-T_9=4.61, P=0.001), took more bites (Paired-T_9=3.95, P=0.003), cleaned a higher number of both clients (Paired-T_9=4.39, P=0.002) and species (Paired-T_9=5.05, P=0.001) and cleaned at a higher rate (Paired-T_9=2.84, P=0.019) than males (Figure 1A–E). Females also initiated a significantly larger proportion of all cleaning events than males (mean ±SD; females: 35.9 ±17.0%, males: 14.1 ±12.7%, Paired-T_{10}=3.53, P=0.005).

Females tended to initiate cleaning events on larger client species than those clients that were initially cleaned by males and those clients that solicited cleaning (client length; female-initiated: 22.5 ±13.2 cm, client- and male-initiated: 9.4 ±2.1 cm, T_{16}=1.95, P=0.069). Furthermore, females tended to initiate a greater proportion of cleaning events as client size increased (r=0.45, N=19, P=0.056) while the proportion of male- and

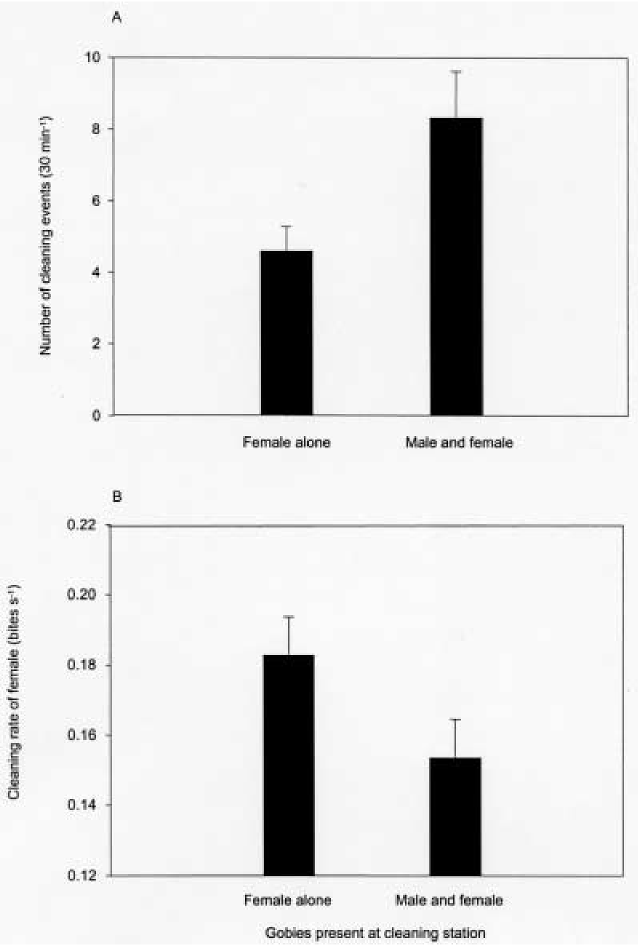

Figure 2. (A) Mean (±SE) number of cleaning events in 30 min; and (B) cleaning rate of female cleaning gobies, when females are alone and when accompanied by a male at the cleaning station (N=11 cleaning stations).

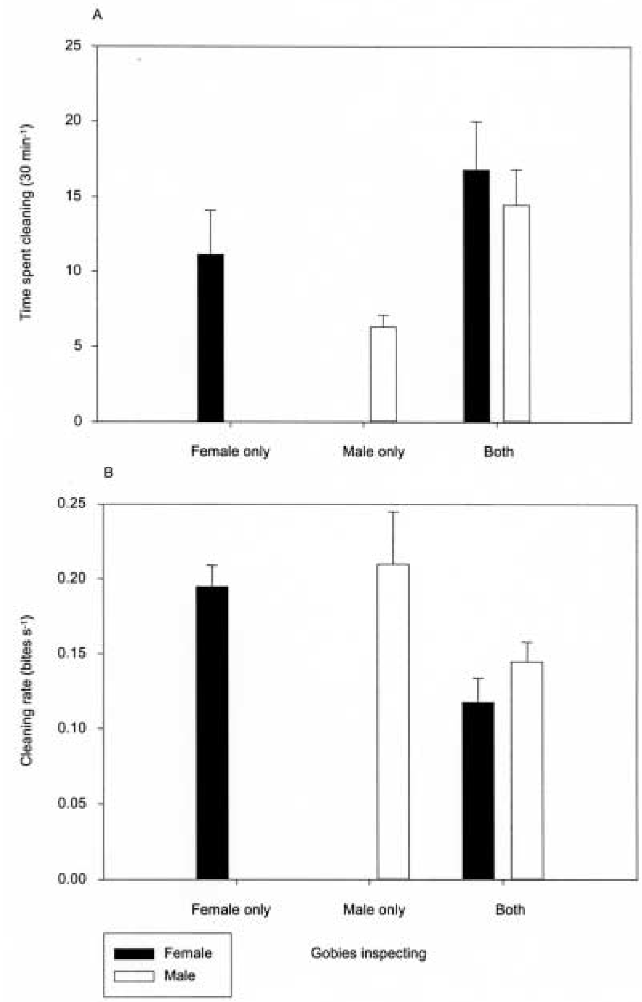

Figure 3. (A) Mean (±SE) time spent cleaning; and (B) cleaning rate of male and female cleaning gobies when cleaning alone and together at their respective cleaning stations (N=11 cleaning stations).

client-initiated events decreased with client size ($r=-0.54$, N=19, $P=0.017$).

The total number of clients inspected at a cleaning station per 30 min was significantly greater when both male and female were present than when the female was alone at a cleaning station (Paired-$T_{10}=2.6$, $P=0.026$, Figure 2A). However, the total time females spent cleaning per 30 min was not significantly different when they were alone and when their male partners were present at the cleaning station, whether males cleaned or not (Paired T-test: $P>0.05$). By contrast, the cleaning rate of females tended to be reduced by the presence of a male at the cleaning station, irrespective of whether the male engaged in cleaning behaviour (Paired-$T_8=2.02$, $P=0.078$, Figure 2B).

When females were alone at a cleaning station the average frequency of client-initiated and female-initiated events was identical (50%). Furthermore, there was no difference in the average length of a cleaning bout, whether client- or goby-initiated (mean ±SD; client-initiated: 12 ±6 s, goby-initiated: 12 ±9 s; Paired T-test: $P<0.05$). However, the cleaning rate of females during client-initiated events tended to be higher than in female-initiated interactions (mean ±SD; client-initiated: 0.2 ±0.05 bites s^{-1}, female-initiated: 0.15 ±0.05 bites s^{-1}; Paired-$T_7=1.97$, $P=0.089$).

Males and females both present at their cleaning stations

At each cleaning station, there was no correlation between the time males spent present at the cleaning station and either their cleaning rate per 30 min ($P>0.05$ in all cases) or their cleaning rate per minute present ($P>0.05$ in all cases). Thus, males did not appear to compensate for time spent away from their cleaning station, perhaps guarding a nest, by increasing their cleaning rates when they were present at the station. Instead, across all sites there was a trend towards higher cleaning rates among males spending more time at a cleaning station ($r=0.56$, N=11, $P=0.075$).

Males spent more time cleaning (Paired-$T_{10}=3.8$, $P=0.003$; Figure 3A) and tended to take more bites per 30 min (Paired-$T_{10}=2.2$, $P=0.052$) when they cleaned with a female than when cleaning alone. In comparison, there was no difference in the time females spent inspecting or the number of bites they took when they were cleaning alone or with a male (Paired-T tests: $P>0.05$, Figure 3A). There was also no significant sex difference in cleaning rate when each sex was cleaning alone, nor was there a significant difference in the cleaning rate of males when cleaning alone and with a female

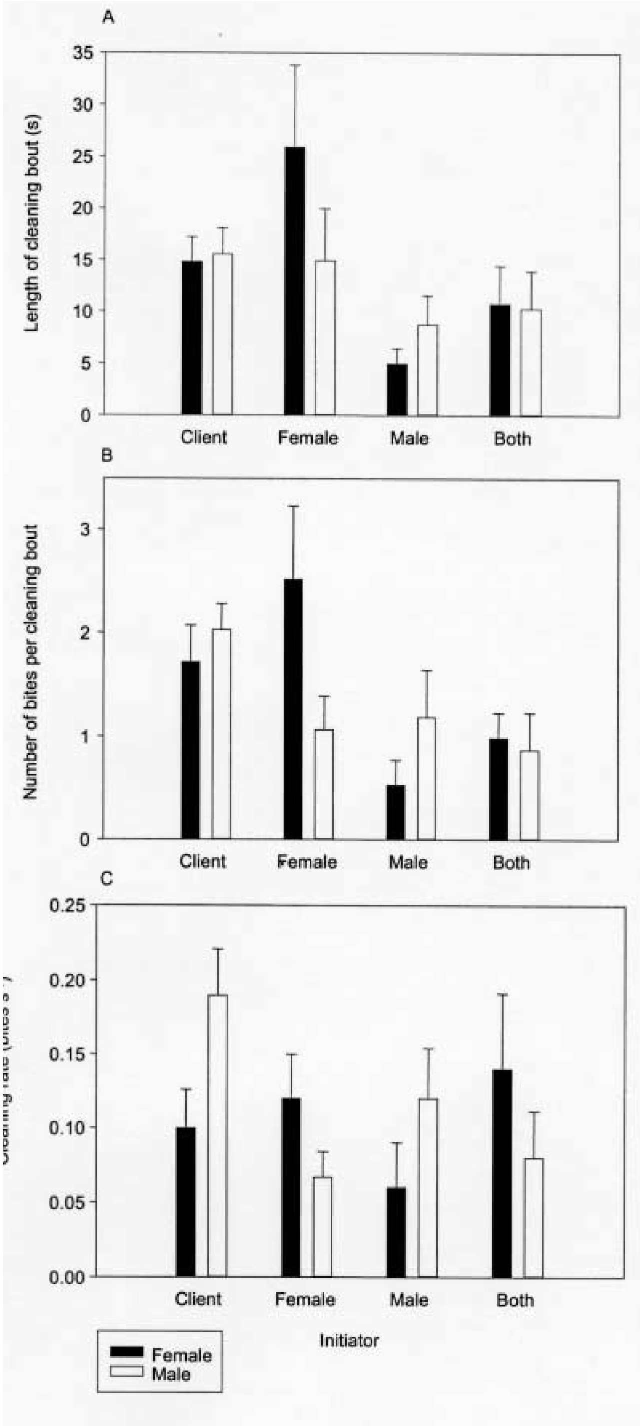

Figure 4. (A) Mean (±SE) length of cleaning bouts; (B) number of bites per cleaning bout; and (C) cleaning rate during cleaning events in which both gobies inspected the client and events were initiated by the client, male cleaning goby, female cleaning goby or both gobies (N=11 cleaning stations).

(Paired T-tests: $P>0.05$; Figure 3B). However, the cleaning rate of females was significantly reduced when cleaning with a male (Paired-$T_{10}=4.36$, $P=0.001$; Figure 3B).

When both gobies were present at a cleaning station but females cleaned alone, there was no significant difference in female cleaning rate between client- and female-initiated interactions (mean ±SD; client-initiated: 0.23 ±0.12 bites s^{-1}, female-initiated: 0.17 ±0.07 bites s^{-1}; Paired T-test: $P>0.05$). Similarly when males cleaned alone there was no difference in cleaning rate between client- and male-initiated interactions (mean ±SD; client-initiated: 0.26 ±0.1 bites s^{-1}; male-initiated: 0.24 ±0.29 bites s^{-1}, Paired T-test: $P>0.05$).

Males and females inspecting the same client

At all sites, cleaning interactions in which both individuals inspected the same client represented a small proportion of both the total time spent together at a cleaning station (mean ±SD: 3.5 ±4.8%) but a relatively greater proportion of the total cleaning time observed per 30 min (28.4 ±19.6%). When cleaning the same client, there was no significant difference in cleaning rate (bites s^{-1}), length of cleaning event or bites taken per cleaning event between males and females (Paired T-tests, $P>0.05$ in all cases). However, if cleaning events are separated according to which individual initiated the interaction, significant differences between the sexes become apparent.

The majority of cleaning events in which gobies inspected together were initiated by clients (62%). Female and male gobies each initiated 15% and 8% of the interactions respectively. Both gobies together initiated the remaining 14% of cleaning events.

When clients initiated a cleaning event, both gobies started inspecting at the same time in 52% of cleaning events while the female gobies were the first to commence inspecting in 22% of events and males in 17%. The cleaning rates of males did not differ whether they responded first or second (mean ±SD; males first: 0.22 ±0.96 bites s^{-1}, males second: 0.17 ±0.09 bites s^{-1}; Paired-$T_4=0.74$, $P=0.5$). Similarly, females starting inspections cleaned at a similar rate as when they inspected second (mean ±SD; females first: 0.13 ±0.07 bites s^{-1}, females second: 0.06 ±0.08 bites s^{-1}; Paired-$T_3=1.92$, $P=0.15$). However, when females responded second their cleaning rate was lower than that of males (mean ±SD; females: 0.09 ±0.14 bites s^{-1}, males: 0.29 ±0.20 bites s^{-1}; Paired-$T_7=3.17$, $P=0.016$). No such sex difference occurred when females responded first (mean ±SD; females: 0.13 ±0.07 bites s^{-1}, males: 0.17 ±0.11 bites s^{-1}; Paired-$T_3=0.88$, $P=0.44$).

When either clients or both gobies together initiated a cleaning event, there was no significant sex difference in time spent on the client or the number of bites taken (Paired T-tests: $P>0.05$ in all cases, Figure 4A,B). However, when females initiated cleaning events they spent significantly more time and took more bites on the client than their mate (length of cleaning bout: Paired-$T_{10}=2.66$, $P=0.024$; bites per cleaning bout: Paired-$T_{10}=2.6$, $P=0.026$; Figure 4A,B). Conversely, if males initiated cleaning interactions they cleaned for longer and took more bites per cleaning event (length of cleaning bout: Paired-$T_{10}=2.24$, $P=0.049$; bites per cleaning bout: Paired-$T_{10}=2.27$, $P=0.046$; Figure 4A,B). Furthermore, females cleaned for significantly longer and took more bites during events they initiated than they did in interactions initiated by males (length: Paired-$T_{10}=-2.58$, $P=0.027$; number of bites: Paired-$T_{10}=2.53$, $P=0.03$; Figure 4A,B).

This apparent advantage to initiating cleaning events is reflected in cleaning rates, at least for females. Females

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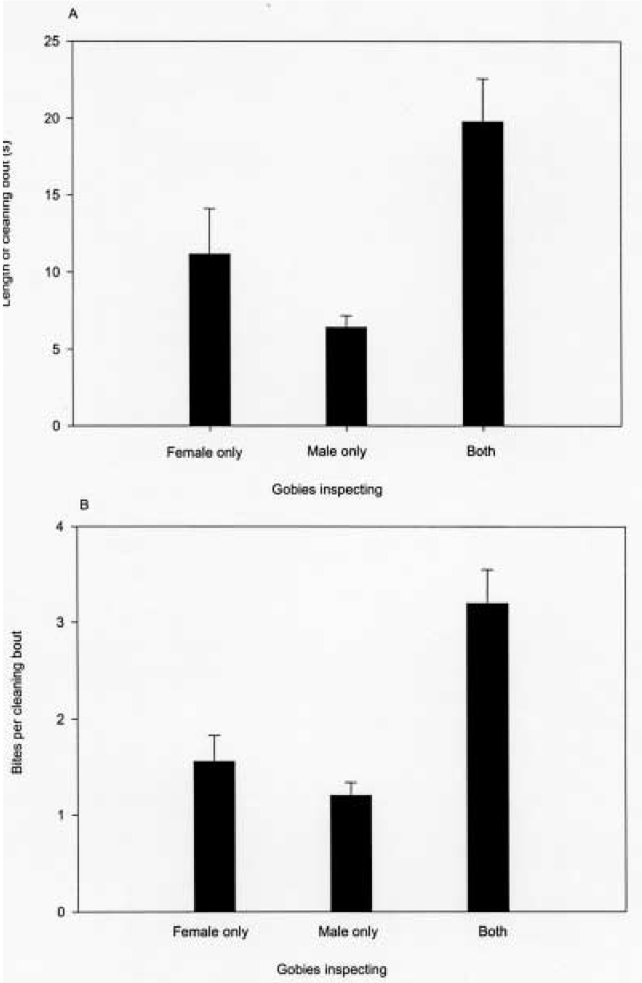

Figure 5. (A) Mean (±SE) length of a cleaning bout; and (B) number of bites taken per client by male and female cleaning gobies when cleaning alone and together at their respective cleaning stations (N=11 cleaning stations).

cleaned at a significantly higher rate than males when the former initiated cleaning events (Paired-T_{10}=2.94, P=0.015; Figure 4C) but there was no difference between the sexes in cleaning rates when males initiated. However, when clients initiated a cleaning event, males then cleaned at a significantly higher rate than females (Paired-T_{10}=3.21, P=0.009; Figure 4C).

There were no significant differences between males and females in the proportion of cleaning events initiated on herbivores, benthic invertebrate predators and planktivores (Paired T-tests: $P>0.05$ in all cases). Unfortunately, fewer than five visits in which both gobies cleaned were made to each cleaning station by piscivorous and omnivorous clients, hence analysis could not be performed on these client trophic types. During inspections on clients there were no significant differences between the sexes in length of cleaning events, number of bites taken or cleaning rate on any client trophic type (Paired T-tests: $P>0.05$).

Client perspective on cleaning interactions

Clients visited cleaning stations more frequently when both gobies were present than when females were alone (Paired-T_{10}=2.6, P=0.026; Figure 2A). Furthermore, the average length of a cleaning bout and the total number of bites taken per client were significantly higher in interactions when both gobies cleaned than when either sex cleaned alone (length: F_{29}=13.26, P=0.002; bites: F_{29}=21.12, $P<0.001$; Figure 5) although there was no difference in cleaning rate (repeated-measures analysis of variance [ANOVA]: $P>0.05$). When both gobies inspected the same client fish, the length of a cleaning bout and the total number of bites taken per client was not significantly different between interactions initiated by females, males, both gobies or the client (repeated measures ANOVAs: $P>0.05$).

Diet analysis

Twelve females and eight males, including four male–female pairs, were collected from cleaning stations located on coral heads. No differences were found between years in the length and weight of gobies or in the number or proportion of each food category (T-tests: $P>0.05$ in all cases). Furthermore, there were no significant differences in the number of scales or gnathiid larvae seen in individuals collected in the morning or afternoon (T-tests: $P>0.05$ in both cases). There were also no differences between the stomach and the intestine in the per cent cover of each food category (Paired T-tests: $P>0.05$ in all cases). These were therefore combined in subsequent analyses.

Females and males did not differ in standard length (females: 22.4 ±2.7 mm, males: 22.3 ±3.8 mm; T_{13}=0.05, P=0.96) or weight (females: 0.14 ±0.08 g, males: 0.15 ±0.07 g; T_{13}=0.34, P=0.74) and there were no significant differences between sexes in the total cover of food in the gut (T_{17}=0.28, P=0.78).

No sex differences were found in the per cent cover of each food category (T-tests: $P>0.05$ in all cases). The largest proportion of the gut was unidentifiable digested material (75.9 ±20.8%). Client-gleaned material accounted for nearly 25% of the total content. This consisted primarily of fish scales (13.2 ±17.8%), gnathiid isopod larvae (8.9 ±13.7%) and parasitic copepods (*Bomolochus* sp. and *Caligus* spp., 1.9 ±4.8%).

Nine of the 12 females and four of the eight males in the sample had ingested gnathiid larvae (χ^2=4.83, P=0.06). Similarly eight of 12 females and four of eight males contained fish scales (χ^2=0.54, P=0.49). A single female ingested a parasitic copepod *Caligus* sp. while one male had ingested a single parasitic copepod *Bomolochus* sp.

In numerical terms, the total number of client-gleaned items tended to be greater in females than in males (T_{14}=2.05, P=0.06). Fish scales and gnathiid larvae were the most abundant food item ingested by both males and females (mean SD; fish scales; females: 7.00 ±11.27 scales, males: 2.75 ±3.33 scales; gnathiid larvae: females: 4.00 ±5.64 larvae, males: 1.25 ±1.49 larvae). The numbers of scales and gnathiid larvae ingested was variable between individuals, ranging from 0–36 and 0–18 respectively, in females, and 0–8 and 0–4 in males. Scales on which the epidermis of the client fish was still visible were present in small numbers (<5) in the stomach of only two fish in the sample. Visible epidermis on scales was not seen in the intestine of any fish suggesting that it may be digested.

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DISCUSSION

Paired male and female *Elacatinus evelynae* show significant differences in cleaning behaviour which appear to be largely related to the presence or absence of males from their cleaning stations and to their cleaning behaviour when present. Overall, females spent five times longer cleaning than males, took more bites on clients, cleaned at a higher rate and also engaged in more cleaning events when both cleaning gobies were present at cleaning stations. These differences in cleaning behaviour tended to be reflected in the diet of males and females but they may be of little consequence for client fish.

Differences between males and females

The sex differences in cleaning behaviour and diet observed here mirror those found for the Mediterranean cleaner wrasse *Symphodus melanocercus*. Females in this species also inspect more clients, spend longer cleaning than males and ingest more items derived from clients than males (Arnal & Morand, 2001a). Such consistent sex differences in cleaning behaviour and diet may be related either to a greater opportunity for cleaning for females or to the relative investment required by each sex in reproduction. Parental care confines male cleaning gobies to their nests for the 4–7 day period of egg development (Thresher, 1984). Males were therefore absent from cleaning stations much more frequently than females and thus had fewer opportunities to partake in cleaning. However, the higher cleaning rate of females observed is inconsistent with foraging differences between the sexes arising only through differing opportunities to clean.

Alternatively, females require a heavier energetic investment in reproduction, which is met through greater cleaning activity. This could be expected of fish species that release their gametes into the water column and provide no parental care. In species with male parental care, however, the discrepancy between the sexes in energetic costs of reproduction is less marked, particularly among polygynous species (e.g. Vandenberghe, 1992; Gonçalves & Almada, 1997). However, in monogamous species such as *E. evelynae*, the energetic cost of reproduction may remain higher for females when, for example, in addition to egg production they take over territorial defence while males are caring for eggs (Okuda, 2001). The costs of reproduction in *E. evelynae* have not been investigated. However, females clean at a higher rate than males and males do not appear to compensate for time spent guarding eggs through increased cleaning rates when present at the cleaning station, suggesting a higher energetic requirement for females in reproduction.

Interactions between males and females

In addition to differences in cleaning behaviour between the sexes, paired gobies also interacted in foraging and altered their cleaning behaviour according to specific circumstances. This potential for direct interaction between males and females does not exist for cleaning species such as *S. melanocercus* since males and females occupy discrete territories and clients are cleaned by a single wrasse during each cleaning bout (Arnal & Morand, 2001a).

The highest potential for interactions occurred when males and females cleaned the same client at the same time. During these relatively rare instances, which nonetheless represented nearly 30% of the time spent cleaning when both gobies were present at their cleaning station, the relative proportion of bites taken by males and females depended on which party initiated the cleaning interaction. Females cleaned for longer, took more bites and cleaned at a higher rate when they initiated cleaning, whereas males appeared to have similar advantages in male- and client-initiated events. Interestingly, the total number of bites taken from a client remained constant, regardless of the initiator's identity. This suggests that an optimal foraging effort may exist per client, probably determined by the client's ectoparasite load. Male and female cleaning gobies then apportioned the available resource, according to first inspection priority. The impact of first inspection priority may be considerable when considered alongside sex differences in client species cleaned. Females initiated a greater proportion of cleaning events on large-bodied clients. In contrast, initiation of cleaning events by clients and males was more likely to involve small client species. Large clients typically carry more parasites (Grutter & Poulin, 1998; Poulin 2000). Females may therefore be actively selecting clients that enable them to meet their apparently high energetic requirements. These results contrast with previous studies which have failed to find a clear preference by *Elacatinus* gobies for large or heavily parasitised clients (Arnal et al., 2000, 2001). Our results suggest that considering individual characteristics of cleaners, including sex, may be critical in understanding patterns of cleaner preferences for specific clients.

Other asymmetric male–female interactions occurred through male presence at a cleaning station. Males spent longer inspecting and took more bites when cleaning the same client as females than when cleaning alone. However, the presence of males, whether cleaning or not, significantly reduced the cleaning rate of females. Therefore, males seem to gain from cleaning with a female but females suffer a foraging cost from male presence. This cost to females is at least partially compensated by increased visits by clients when both cleaners are present at the cleaning station. In general, decreased foraging by females can have significant impacts on reproduction. Lowered energy intake has previously been shown reduce female batch fecundity (e.g. convict cichlids; Townshend & Wootton, 1984), total breeding season fecundity (e.g. sticklebacks; Fletcher & Wootton, 1995) and increase female spawning interval (e.g. sticklebacks; Ali & Wootton, 1999). If a reduced female feeding rate effectively translates into a decline in absolute food intake, the reproductive potential of both partners could be affected.

The impact of male presence on female cleaning activity could have consequences for female mate choice. For example, if the cleaning behaviour of males is affected by size, females should consider both the ability of a male to provide care and his impact on female foraging. Large males may score highly on both counts, attracting more clients to a cleaning station as well as being better fathers. For example, larger males in the goby *Valenciennea strigata* (Broussonet, 1782) provide a greater share of burrow maintenance allowing females to feed for longer (Reavis & Barlow, 1998). However, large males may have a greater impact on female cleaning rate since larger individuals require more energy. Large males could, therefore, be as likely to cause a decrease as an increase in female foraging efficiency. Overall, in socially monogamous species, where males and females occupy the same territories and forage together, both male and female choice of mate should reflect not only the ability of each sex to reproduce or provide care but also the impact of either sex on non-reproductive behaviours such as foraging.

Client perspective

From the perspective of a client visiting a cleaning station, the behaviour of cleaners has the potential to have a significant impact on the cleaning service provided. Recent studies investigating the factors motivating clients to seek cleaners have illustrated that clients seek cleaners for ectoparasite removal (Arnal & Morand, 2001b; Grutter, 2001; Arnal et al., 2001). Clients should therefore show a preference for cleaners that provide the highest quality cleaning service.

Clients visiting a cleaning station at which both gobies were present potentially received a higher quality service as both the time spent inspecting and the number of bites taken in each cleaning bout were greater than if either sex inspected alone. Indeed, clients visited cleaning stations more frequently when both gobies were present. However, it is unclear whether a long cleaning event represents a high quality cleaning service. Increased inspection time may increase the likelihood that cleaners take bites of mucus or scales rather than removing ectoparasites. Furthermore, if posing at a cleaning station increases predation risk for clients, a high cleaning rate rather than long cleaning bouts should be preferred. However, in our case, cleaning rate was not significantly affected by which gobies engaged in cleaning. In addition, when both gobies were present at a cleaning station, interactions between males and females revolved around reapportioning the service provided rather than changing the total service. Thus, interactions between cleaners may have little overall effect on client preference for specific cleaning stations.

Our results show that using an individual-based perspective on behaviour can offer new insights into well-studied systems such as cleaning symbioses. We have found that male and female cleaning gobies exhibit differences, interactions and conflicts in foraging, which have been previously overlooked. These differences explain, for example, why previous studies failed to find a clear preference by *Elacatinus* gobies for large or heavily parasitized clients (Arnal et al., 2000, 2001). We have shown that only females exhibit this predicted preference. Considering individual characteristics of cleaners, including sex, may thus be critical for understanding key aspects of cleaning symbioses, such as patterns of cleaner preference for specific clients, and also for generating new directions for future work.

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