More aggressive sea turtles win fights over foraging resources independent of body size and years of presence

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ARTICLE INFO

Article history:
Received 27 August 2021
Initial acceptance 11 October 2021
Final acceptance 4 April 2022
Available online 10 June 2022
MS. number: 21-00501R

Keywords:
agonistic interaction
competition
habitat complexity
ideal free distribution
repeated interaction
territoriality

Interactions among individuals of the same species inform us about resource value and sociality; however, for species that are difficult to observe directly, these behaviours are potentially missed or misinterpreted via remote monitoring approaches. Here, we investigated how agonistic interactions influenced temporal and spatial variation in the social structuring of loggerhead sea turtles, Caretta caretta, foraging on sponges at a reef (Zakynthos, Greece) over multiple years. We directly observed individuals via snorkel surveys (with photoidentification and videos) supported by aerial drone surveys. Most turtles were immature loggerheads, of which half were detected in more than 1 year. Individual loggerheads occupied distinct (very small) patches on the reef, with low overlap when foraging. Interactions generally occurred when loggerheads were adjacent to, or passing through, patches occupied by other individuals. Interactions between loggerheads represented an extremely small fraction of the activity budget, but potentially consumed two to three times more energy than swimming and foraging. Escalation of aggression, unexpectedly, skipped the passive (evaluation) phase in half of interactions (starting with biting and chasing), with contests being primarily won by more aggressive individuals, independent of body size and duration of presence (i.e. reef occupancy in years). Distinct hierarchical structuring was detected based on win outcomes and spatial area use within each year; however, the number and combination of turtles frequenting the reef varied across years, with individuals only dominating for 2–3 years before departing (or returning intermittently) and being replaced. The unexpected fight dynamics and regularly changing hierarchies indicate that individuals perceived the resource value of sponges differently, which was attributed to differences in their ability to assess resource abundance and/or availability of resources at alternative sites. Our results contribute to the emerging field of sociality in reptiles.

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The perceived energetic value of a resource, such as food, is generally assumed to determine the extent to which individuals in a species compete for access, which may differ with state of hunger or assessment ability, resulting in individuals behaving differently over the same resource (Clark & Ehlinger, 1987; Arnott & Elwood, 2008; Wolf & Weissing, 2012; Bradbury & Vehrencamp, 2014). In confrontations, individuals typically evaluate (passive phase) and, sometimes, escalate to agonistic behaviour (physically aggressive phase) to test the opponent’s ability. Competitive ability and occupancy of a territory tend to determine the outcomes of interactions (game theory, Parker, 1974; Enquist & Leimar, 1983; Maynard Smith, 1982, 1994); however, between-individual differences might also have an impact (Dingemanse & Wolf, 2013; Fuxjager et al., 2010). Repeated interactions among the same individuals result in the establishment of hierarchies for access to resources (Bell et al., 2009; Petrie, 1984), with animals distributing themselves in a way that reduces, often energetically expensive, competition (ideal free distribution, Fretwell, 1972; Parker & Sutherland, 1986). Thus, quantifying the extent and consistency of agonistic interactions among individuals provides information on...
resource value, individual behavioural syndromes (or personality) and social hierarchies, as well as insights on functional significance during development and evolution (Biro & Stamps, 2008; Wolf & Weissing, 2012; Bradbury & Vehrencamp, 2014; Griffin et al., 2015).

Acquiring direct observations of repeated social interactions among the same and different opponents in the natural environment is particularly difficult for certain animal groups, including reptiles and marine megafauna, such as sea turtles (Castelblanco-Martinez et al., 2019; Hays et al., 2016). This limits our understanding of the diversity and complexity of behaviours that potentially exist and the extent of behavioural plasticity in responses (DeWitt et al., 1998; Dingemanse & Wolf, 2013; Shi et al., 2004). For instance, much of our understanding of wide-ranging marine megafauna is restricted to inferences made from remote technologies, such as logging and tracking devices, which provide vertical and horizontal movement patterns of tagged individuals (Hays et al., 2016). While some studies have validated these data sets in relation to certain behaviours through direct observations or emerging imagery-based technologies (e.g. Jeanet et al., 2020; Thomson et al., 2011), cost limits the number of animals that can be tracked remotely, hindering our understanding of how individuals share space with other animals at very fine scales (Kays et al., 2015; Secor et al., 2019). Intraspecific numbers of studies using infra-red based technologies are demonstrating the complexity of intra- and interspecies interactions in shaping ecosystems, including animal-borne cameras, fixed-substrate cameras (e.g. BRUVs) and mobile cameras, both underwater and above water (Castelblanco-Martinez et al., 2019; Schofield et al., 2019; Thomson et al., 2011). These visual approaches also allow the long-term monitoring of individuals via photoidentification, which is based on easily detectable natural markings (e.g. flukes, whiskers, scale patterns), is reliable over long timescales (multiple years) and can be augmented with citizen science (Holmberg et al., 2008; Papafitsoros et al., 2021).

Sea turtles are one of the most widely monitored marine megafauna groups globally, with information on over 7000 tracked individuals of all seven species having been published over the last 25 years (Hays & Hawkes, 2018). These tracking studies have demonstrated phenotypic plasticity in the context of movement patterns related to both foraging and breeding habitat use (Dujon et al., 2018; Foisseau et al., 2012; Hatase et al., 2007; Hawkes et al., 2006). However, our understanding of social interactions remains limited, due to the difficulty of monitoring groups of individuals over extended periods in the marine environment (Gaos et al., 2021; Schofield et al., 2019). Social interactions among adult individuals during breeding have been widely recorded, including male–male, male–female and female–female encounters via direct observation and aerial (aeroplane and unmanned drone) surveys (for a review, see Schofield et al., 2006), as well as interactions over access to fish-cleaning stations (Schofield, Papafitsoros, et al., 2017). In contrast, detailed accounts of interactions during foraging, which encompasses most of the life history of sea turtles, even as adults, remains limited. Remote and acoustic tracking studies show that the foraging home ranges of multiple individuals overlap for loggerhead, Caretta caretta, green, Chelonia mydas, and hawksbill, Eretmochelys imbricata, turtles (Chevis et al., 2016; Christiansen et al., 2017; Dujon et al., 2018), leading to assumptions of passive coexistence. However, intense competition over patches within home ranges has been directly observed for individuals from these three species too, and likely also exists in the other four species (Dujon et al., 2018; Fujisaki et al., 2016; Gaos et al., 2021; Limps & Limps, 2003; Schofield et al., 2006; Smolowitz et al., 2015; Thomson et al., 2015). Thus, long-term observations of sea turtles at foraging sites, including multiple repeated interactions among known individuals, are required to understand how this behaviour contributes to the foraging ecology of sea turtles, and how it compares to that documented for other wildlife.

Here, we used a combination of direct observations, photo-identification and aerial drone surveys to quantify how agonistic interactions influenced temporal and spatial variation in the social structuring of loggerhead sea turtles at a foraging site over 11 years (2011–2021). We hypothesized that larger (stronger) turtles would win more interactions and would be more aggressive with longer occupancy (across years) at the site. We also hypothesized that the social hierarchy and distribution of turtles within the site would be organized around these individuals. The behaviour of individuals occupying the site was recorded with videos and photographs, and an established database was used for photoidentification (Schofield et al., 2008, 2020). Our results are expected to demonstrate how social interactions influence the use of foraging resources by sea turtles and associated life history implications for survival and fitness.

**METHODS**

**Study Site and Species**

Laganas Bay on Zakynthos Island, Greece (37°43’N, 20°52’E; Fig. 1a) is a major rookery for loggerhead sea turtles, supporting approximately 100 and 250 breeding males and females annually, respectively (Casale & Margaritoulis 2010; Margaritoulis et al., 2003; Schofield, Katselidis, et al., 2017). However, tracking studies and long-term photoidentification have confirmed that this area also provides foraging habitat for resident adult male loggerheads and immature loggerhead and green turtles (Schofield et al., 2009, 2020; Dujon et al., 2018; Papafitsoros et al., 2021). Since 1991, Laganas Bay has been protected by Greek legislation and under the framework of the National Marine Park of Zakynthos from 1999. Within the maritime zoning, underwater fishing and trawling are prohibited year-round, while special sea turtle protection measures are in place from 1 May to 31 October (breeding period), with respect to boat speed and anchoring. However, the study site falls within maritime zone C where boat speeds are restricted to 6 knots. This study focused on an isolated reef (directly adjacent to Cameo Islet; Fig. 1a and b) frequented by multiple immature and adult turtles (Papafitsoros & Schofield, 2016; Papafitsoros et al., 2021; Fig. 1a, b, d) foraging on the sponge Chondrilla nucula (Porifera, Demospongiae; Fig. 1c).

**Inwater Surveys**

The reef at Cameo Islet was surveyed between April and October 2011 to 2021. Photographs and videos collected by our group were used to record the presence and encounters of turtles frequenting the reef. The identity of all individuals could be distinguished from facial scute patterns, due to their small numbers and repeated encounters, as well as additional distinguishing features (scars, distinctive markings and/or within-year barnacle distributions on carapaces). These records were supplemented with social media videos in 2018–2021. Social media videos were only used when (1) the year and location were confirmed, (2) individuals could be identified and (3) the outcome could be determined. In July–August of 2018 and 2019, intensive snorkel-swim surveys were conducted to calculate activity budgets, during which focal turtles were continuously monitored by hand-held video cameras (GoPro Hero 4) until the animal departed or until a session was complete (2 h on average, spread between 0700 and 2000, daylight hours). Surveys were conducted on fair weather days only (<4 Beaufort Scale; >5 m underwater visibility). At the start of each survey, the entire reef with sponges was searched to document all individuals present, then focal individuals were monitored. The reef was rechecked at 1 h intervals to document any new
Aerial Drone Surveys

Aerial drone surveys were conducted during July–August 2018 (five dates) and June–July 2019 (six dates) to evaluate the area used by the turtles. A DJI Phantom 3 Professional (www.dji.com) was preprogrammed to hover at 60 m altitude (allowing 100 m field of view; see Schofield, Katselidis, et al., 2017; Schofield, Papafitisoros, et al., 2017 for methodological details) over the reef for four consecutive 15 min periods (duration of each battery; totalling 60 min footage per survey date). We recorded the positions of turtles at 1 min intervals (Dujon et al., 2021) and noted any interactions. Immediately before and after each survey, we collected photographic images of turtles at the patch for photoidentification and to compare the locations they frequented. The 50% kernel utilization distribution (KUD; Worton, 1989; Seaman & Powell, 1996) was used to calculate the area used by each turtle during each survey, and overall. All 50% KUDs were calculated using the adehabitatHR package (Calenge, 2006) and plotted in R (R Core Team, 2020), using the reference bandwidth as the chosen smoothing parameter. This package requires at least five locations to produce a KUD.

Ethical Note

Approval to conduct inwater research of sea turtles was given by the Greek Ministry of Environment (Permit: 151503/162 and 181806/941). This was solely an observational study in a tourism area and did not involve any disturbance.

Data Analysis

Facial scute images of all individuals were extracted from photographs and video footage and were matched to a previously validated long-term photoidentification database (2000–2021) containing over 1400 uniquely identified turtles frequenting Laganas Bay (Papafitisoros et al., 2021; Schofield et al., 2008, 2020). Body length measurements (curved carapace length, CCL in cm) were obtained with an elastically tape measure for seven repeatedly sighted turtles. The relative size of all other turtles was estimated from still frames showing the lateral body view of measured turtles interacting with unmeasured turtles when directly adjacent. We validated that the means of still-frame estimates were accurate to within 5 cm based on measured individuals. External sexual characteristics in sea turtles emerge as they mature, with tail elongation being a key characteristic allowing the discrimination of adult males and females (Casale et al. 2005; Rees et al. 2013). We categorized as males (immature or adult) those individuals with tails protruding >6 cm beyond the carapace (Rees et al. 2013) and they were only categorized as adults if they had been recorded mating. Adult females were categorized as any individuals with external flipper tags (attached after nesting on beaches) or recorded being mated. It was not possible to discriminate immature females.

All videos capturing turtle behaviour between consecutive breathing bouts were processed (around 10–30 min intervals). Behaviour was recorded at 5 s intervals to document the relative time spent engaging in each activity (foraging, swimming and interactions), as well as breathing bouts and flipper beats. Foraging was defined as behaviour that involved directly eating sponges from the reef. Swimming was defined as horizontal movement in the water column between two different foraging locations. Interactions were defined as when visual contact was made between one or both turtles until separation (departure of one or both individuals from the patch). For each behavioural category, energy expenditures were inferred from the number of flipper beats and breathing bouts documented (Dudley et al., 2014; Hays et al., 2007).

To evaluate the structure of interactions (contest escalation), we recorded the stage of escalation and ordering of the stages based on existing studies of animals (Maynard Smith, 1994; Parker, 1974), including sea turtles (Schofield et al., 2007). These stages were (1) initial contact, involving visual or tactile cues of one or both individuals, (2) passive phase, nonaggressive confrontation involving
wide head—tail circling, with individuals keeping a distance of about 1 m from one another and visually assessing the opponent, (3) aggressive phase, aggressive confrontation involving close chasing and physical contact such as biting and (4) separation, with either both turtles swimming away in different directions (mutual) or one fleeing and the other chasing (loser and winner, respectively). Avoidance interactions were those in which just one turtle sighted another during level (1), but immediately changed direction and moved out of visual range. In a small number of instances, two turtles were recorded foraging in the observer’s line of sight; this was recorded as foraging as it was not possible to validate whether turtles were aware of each other’s presence until an interaction arose, which was usually when one or both surfaced to breathe.

To construct dominance hierarchies, we used David’s score because of the small group sizes at the reef in each year (David, 1987; Gamell et al., 2003; de Vries, 1998, 2006). In brief, the David’s score was calculated for each individual out of the group of individuals present within each year, based on the observed number of dyadic wins and losses (for details, see David, 1987; de Vries, 1998). Because the number and frequency of interactions varied significantly between dyads, de Vries’ correction for chance was used (de Vries, 1998). The statistical significance of the hierarchy was tested by calculating the steepness measure of interactions following de Vries et al. (2006), and David’s score was normalized to fall between 0 and 1. Dominance hierarchies were only constructed for 2015–2021, as no interactions were recorded during 2011–2014. To identify which factors determined the outcomes of contests, we recorded the individuals that fought, status of individuals (patch resident versus intruder), duration of presence at the reef (years), body size, degree of escalation (passive versus aggressive), aggression (number of bites) and outcome (winner, loser, mutual). We also evaluated the level of aggression exhibited by each individual to the same opponent in repeated interactions and to different opponents.

Statistical Analyses

We used the chi-square test for given probabilities (goodness of fit) to investigate the relative proportions of the three behavioural categories (foraging, swimming, interactions) and inferred energy expenditure based on the number of flipper beats and number of breaths per minute. We used Fisher’s exact test to compare the escalation of interactions during foraging versus breeding. In addition, because data on the same individuals were collected over multiple years, we used linear mixed-effects models, with individual turtles and time as random effects (within individuals and time). Generalized linear mixed-effects models with binomial family were used to investigate potential associations of the fight variables with fight outcomes. We used analysis of deviance (type II Wald chi-square tests) to further examine these models. We set significance at P < 0.05. Descriptive statistics are presented as mean ± SD. For all statistical analyses, we used R (R Core Team, 2020).

RESULTS

Between 2011 and 2021, 42 unique sea turtles (of which one was a green turtle) were recorded frequenting the reef (Table A1). Thirty-eight loggerhead turtles were immature (sex only determined for 13 individuals [males]; Table A1) and three were adults (two males and one female; Table A1), with an estimated CCL of 30–85 cm. Fifty-two per cent of turtles were only observed foraging during 2018 and six of the 9–13 turtles (recorded foraging versus generally present in the area, respectively) detected in 2019 (five surveys in 2018 and six in 2019; Fig. 2, Table A1). Only two turtles (Turtle 12 and 3) were detected in aerial drone surveys in both years. During the dominant turtle differing in 2018 (Turtle 2) and 2019 (Turtle 20), both individuals occupied the same patch on the reef (Fig. 2b, c, d, e, red shading). The other turtles were distributed at patches surrounding that used by the dominant turtle. Multiple surveys of the same individuals within each year showed that they exhibited high fidelity to a patch (mean 10 ± 9 m distance between the midpoint of each 50% KUD, with overlapping or proximate KUD areas (Fig. 2d and e). The 50% KUD area for each turtle was a mean of 0.09 ± 0.11 km² for individual surveys and an overall 0.71 ± 0.95 km² for all surveys combined. Interactions occurred when two turtles were on the boundaries of their patches, or when turtles passed through occupied areas (Fig. 2a).

Activity Budgets

Based on 909 min of video footage of turtles collected during the 2018–2019 focal surveys, turtles spent significantly more time foraging (68%) than swimming (31%) or interacting (1%; χ² = 67.58, P < 0.01; Fig. 3a). Flipper beats and breathing bouts were two to three times higher during interactions (50 beats/min; 2.5 breaths/min) than during swimming and foraging (22 and 19 beats/min; 0.75 and 0.25 breaths/min, respectively; Fig. 3b), with these differences being significant (flipper beats/min: χ² = 24.938, P < 0.01; breaths/min: χ² = 143.57, P < 0.01). Interactions (from sighting to separation) lasted 0.86 ± 0.66 min on average.

Escalation of Aggression

Just 4% of interactions were resolved during the passive phase (see Supplementary Video S1), with 70% of interactions involving aggression. However, while 22% of interactions passed through a passive (circling) phase before initiating aggression (see Supplementary Video S2), 48% of interactions were immediately physically aggressive (no passive phase; see Supplementary Video S3), with this being significantly higher than the other types of escalation (χ² = 10.778, P = 0.01; Fig. 4a). In 26% of cases, interactions were avoided, either by the intruder sighting the resident and departing immediately or visual contact by both but no action.

The escalation of interactions during foraging was significantly different to that during breeding (Fisher’s exact test: P < 0.01). Comparison with aggression recorded between adult females over transient thermal hotspots during breeding (Fig. 4b; Schofield et al., 2007) demonstrated that, while both groups showed similar levels of avoidance to initiate interactions (26% and 23% for foraging versus thermal, respectively), passive resolution prevailed in female–female interactions (57%), with no cases of aggression without the preliminary passive phase.
Dominance and Aggression

David's scores obtained for all contests between 2015 and 2021 showed clear hierarchical structuring among turtles within each year (Fig. 5, Table A2). Three turtles were clearly dominant for 2–3 years each over this period, with their positions in the ranking being clearly separated from all other turtles (Turtle 1, 2, 20; Fig. 5). This result is supported by the wins data, with these three turtles winning all fights (except one fight for Turtle 1). Yet, after just 2 years, Turtles 1 and 2 were displaced; Turtle 1 returned...
intermittently to the reef in 2017 before being killed by boat strike, while Turtle 2 was not detected again after 2018. In contrast, the ranking of long-term residents (>5 years) was consistently lower, and likely fluctuated depending on which individuals and number of individuals were present (Fig. 5; Table A2). Of note, the steepness of the hierarchy was strongly correlated with the number of individuals present, and this index was treated with caution (Fig. A1).

The generalized linear mixed-effects model showed that the outcomes of contests were not significantly affected by body size or duration of presence (years) on the reef ($P > 0.15$; Table A3). Turtles that won contests were typically the resident of the patch being fought over ($P < 0.05$) and were more aggressive with a higher number of bites than the opponent ($P < 0.01$; Table A3). These findings were supported by the fact that, in some years, smaller turtles dominated the reef (e.g. Turtle 20), and that the turtles with the greatest duration of reef occupancy tended to be consistently lower in the hierarchy, and vice versa. For instance, in 2019 the most dominant turtle was the smallest that year (Turtle 20; 30–40 cm), and consistently won interactions against much larger turtles (up to 60–70 cm CCL). In comparison, the dominant turtle (Turtle 2) in 2018 was one of the largest immature turtles (60–70 cm CCL), but also won interactions against larger, adult turtles (70–85 cm CCL).

For the same turtle pairs, repeated interactions were generally of a similar aggression level (number of bites; 73% of cases for 21 different pairs with repeated interactions). However, the level of aggression changed with the opponent (based on nine turtles each interacting with two to seven different turtles). For example, the most aggressive turtle in 2018, Turtle 2, showed a consistently high level of physical aggression (100%, i.e. all fights; mean 12.3 bites/interaction; maximum 29 bites/interaction) towards Turtle 13, but exhibited intermediate aggression to Turtle 12 (mean 2 bites/interaction). However, more data are required to validate these observations statistically.

**DISCUSSION**

Our long-term, direct observations of sea turtles at a foraging site demonstrated their investment in complex social interactions and dynamic social structuring. Turtles frequenting the reef foraged in distinct patches, with agonistic interactions appearing to regulate how individuals were distributed across the site. Unexpectedly, while the most dominant turtle was typically the most aggressive, it was not necessarily the largest nor longest resident of the site across years. Interestingly, turtles were only dominant for 2–3 years, with other turtles already present in the hierarchy ascending to this position (Turtle 2 and Turtle 20; Tables A1, A2). Furthermore, the passive ‘assessment’ phase was frequently skipped (with immediate aggression) in repeated interactions between the same individuals, indicating familiarity (recognition). Our results provide...
new insights on the foraging ecology of sea turtles, and the importance of directly observing individuals in relation to conspecifics and the surrounding environment.

Our aerial drone surveys showed that turtles foraged in very fine-scale, nonoverlapping patches. Despite major advances in remote technologies over the last 20 years (Hays & Hawkes, 2018; Kays et al., 2015; Sequeira et al., 2019), discriminating such fine-scale area use by individual animals is still not possible, leading to assumptions of shared, noncompetitive patch use (Chevis et al., 2016; Christiansen et al., 2017; Hays et al., 2016). Even when tracking turtles with Fastloc GPS transmitters, location accuracies of 20 m or more would fail to capture the segregation of individuals occupying very small sites (Dujon et al., 2018). Thus, it is important to integrate multiple technologies to confirm area used and associated behaviours, including some form of direct observations (Castelblanco-Martínez et al., 2019; Schofield et al., 2019; Thomson et al., 2011). The seven species of sea turtles forage on a variety of resources in benthic to oceanic habitats (Hatase et al., 2007; Smolowitz et al., 2015; Rees et al., 2016); thus, as video records accumulate on the frequency and intensity of interactions in the coming years due to advances in such technologies (remote and animal borne; Thomson et al., 2011; Smolowitz et al., 2015; Castelblanco-Martínez et al., 2019), this will open up opportunities to evaluate perceived resource value within and across species in relation to different resources (Hays et al., 2016). This information would allow us to quantify the importance of different foraging habitats to turtles and objectively implement the protection effort required (Anthony & Blumstein, 2000; Gaos et al., 2021; Hays et al., 2019). This is particularly pressing regarding sea turtles, as most protection effort remains focused on nesting habitats (Rees et al., 2016; Mazaris et al., 2017), with more effort being needed to delineate and protect foraging habitats appropriately.

Unexpectedly, the passive (evaluation) phase was skipped in half of the encounters at the foraging site; instead, aggressive behaviour occurred immediately. In contrast, most interactions were resolved at the passive phase for adult female–female and adult male–male interactions during breeding (Schofield et al., 2006, 2007), supporting general expectations that animals retreat rather than escalate to avoid injury and or the loss of energy reserves (Parker, 1974; Enquist 1983; Maynard Smith, 1982, 1994). However, immediate aggression has been documented in males when in the presence of receptive females during breeding in various species (DiMarco & Hanlon, 1997). This difference in escalation recorded at our site might be attributed to differences in perceived resource value (Clark & Elingher, 1987; Wolf & Weissing, 2012; Sih et al., 2014) or differences in repeated encounter rates between the same individuals (Griffiths & Magurran, 1997). For instance, there are around 250 females and 100 males frequenting the breeding area in Laganas Bay (6 km coastline) in a given season (Schofield, Papafitsoros et al., 2017a, 2017b, 2021), whereas fewer than 15 individuals frequented the foraging reef (Fig. 1) each year, with high fidelity to specific patches. This likely facilitated repeated interactions and increased familiarity, influencing decision making (Krause et al., 2000). Increased familiarity might speed up decision making, avoiding time investments in passive evaluations (Fuxjager et al., 2010). In fact, interactions among turtles at the foraging site were >2.5 min shorter than those of adult females during breeding on average (means 0.86 min versus 3.4 min, respectively), with fast outcomes potentially allowing a faster return to foraging. This aggressive confrontation structure might be a result of age or inexperience, with most turtles at the foraging site being immature, with greater need to access resources for growth driving aggressive interactions (Stamps & Groothuis, 2010). Immediate aggression towards a previously aggressive opponent might also give (smaller) individuals an advantage in resource protection, and potentially reduce the risk of future attack, with smaller individuals often escalating agonistic interactions faster (Scheeder & Huber, 2001).

Behaviour is also predicted to be more consistent with familiar individuals (repeatedly encountered) than with unfamiliar individuals (Wolf & Weissing, 2012; Sih et al., 2014; Griffin et al., 2015), as the relative dominance between pairs of familiar individuals would have been previously ascertained (dear enemy syndrome; Petrie, 1984). This might also explain why some individuals were foraging in relatively close proximity to one another, while not interacting or only intermittently, with generally mutual resolution. Social hierarchies constructed from contest outcomes showed that dominant individuals were clearly separated (steepness) from all other individuals frequenting the reef and tended to be the most aggressive, but with very frequent turnover (~3 years). In contrast, the ranking of long-term residents (~5 years) was consistently lower, and likely fluctuated depending on which individuals and number of individuals were present. Aerial drone surveys showed that successive dominant individuals frequented a specific patch, with the other individuals occupying surrounding patches, with generally high fidelity within years (Fig. 2). These distributions correspond well to the ideal free distribution (Fretwell, 1972; Parker & Sutherland, 1986), as interactions accounted for the smallest part of the activity budget, and only occurred when turtles were in visual range at the boundaries of patches, or when passing through. While the social hierarchy within a given year was fairly stable, this changed across years due to the presence of different combinations of turtles. The occupancy of peripheral patches might represent a trade-off between patch quality and energy allocation to interactions (Searle et al., 2005; Stephens & Krebs, 1986, p. 262), supporting the notion that interactions are energetically costly.

Our study showed that the aggressiveness of individuals drove dominance; however, these individuals were not necessarily larger, which contrasted with the expectations of evolutionary competition models (Maynard Smith, 1982, 1994). Smaller individuals initiating aggression in contests has been attributed to their having no alternatives (desperado effect) or perception errors (Grafen, 1987). However, Morrell et al. (2005) showed that more aggressive smaller individuals could win more contests when resources are abundant, as larger individuals might choose to avoid the cost of fighting and seek alternative uncontested resources. This is a possibility at our study site, as multiple foraging sites exist within

Figure 5. Relative ranking of loggerhead turtles, Caretta caretta, to the dominant turtle (ranked 1) in the reef hierarchy based on David’s score (Table A2) for 2015–2021. Only turtles that were involved in contests were recorded here, not all turtles recorded on the reef (Table A1). All David’s scores were adjusted to fall between 0 and 1 to allow comparison. Turtles frequenting the reef in consecutive years are presented as lines of 20 m or more would fail to capture the segregation of individuals occupying very small sites (Dujon et al., 2018). Thus, it is important to integrate multiple technologies to confirm area used and associated behaviours, including some form of direct observations (Castelblanco-Martínez et al., 2019; Schofield et al., 2019; Thomson et al., 2011). The seven species of sea turtles forage on a variety of resources in benthic to oceanic habitats (Hatase et al., 2007; Smolowitz et al., 2015; Rees et al., 2016); thus, as video records accumulate on the frequency and intensity of interactions in the coming years due to advances in such technologies (remote and animal borne; Thomson et al., 2011; Smolowitz et al., 2015; Castelblanco-Martínez et al., 2019), this will open up opportunities to evaluate perceived resource value within and across species in relation to different resources (Hays et al., 2016). This information would allow us to quantify the importance of different foraging habitats to turtles and objectively implement the protection effort required (Anthony & Blumstein, 2000; Gaos et al., 2021; Hays et al., 2019). This is particularly pressing regarding sea turtles, as most protection effort remains focused on nesting habitats (Rees et al., 2016; Mazaris et al., 2017), with more effort being needed to delineate and protect foraging habitats appropriately.

Unexpectedly, the passive (evaluation) phase was skipped in half of the encounters at the foraging site; instead, aggressive behaviour occurred immediately. In contrast, most interactions were resolved at the passive phase for adult female–female and adult male–male interactions during breeding (Schofield et al., 2006, 2007), supporting general expectations that animals retreat rather than escalate to avoid injury and or the loss of energy reserves (Parker, 1974; Enquist 1983; Maynard Smith, 1982, 1994). However, immediate aggression has been documented in males when in the presence of receptive females during breeding in various species (DiMarco & Hanlon, 1997). This difference in
Laganas Bay and around Zakynthos Island, as well as on the neighbouring islands and mainland (Dujon et al., 2018), with different locations potentially supporting different food items of different availability and energetic value (Searle et al., 2005; Seidel & Boyce, 2016). Furthermore, two of the dominant individuals ceased being dominant after 2 years (one frequented the reef intermittently in 2017 before being killed byboat strike, and the other was not recorded at all in 2019–2021). This might be attributed to increased risk of mortality or fatigue (Buwalda et al., 2013) or changes to perceived resource value (Fuxjager et al., 2010; Dingemanse & Wolf, 2013), resulting in their switching to alternative sites with lower competition pressure. For instance, dominant turtles were involved in twice as many interactions than average, implying greater energy expenditure and potential negative impacts on survival and biological fitness (Milton & Lutz, 2003; Biro & Stamps, 2008; Wolf & Weissing, 2012). Stress hormones (e.g. corticosterone) produced during antagonistic interactions can have harmful physiological effects on turtles, including reducing blood glucose levels and inhibiting immune and salt gland functions (Milton & Lutz, 2003; Jessop & Hamann, 2005). One long-term resident of the foraging site (Turtle 12) was recorded foraging on the coast of mainland Greece in 2021 (Papafitsoros, 2022), while two others were killed by propeller injuries in Laganas Bay in 2017 and 2019 (Turtle 1, at this point only intermittently frequenting the reef, and Turtle 6; Table A1; Papafitsoros et al., 2021), demonstrating the importance of establishing the fate of these individuals. Furthermore, the turtles in our study were foraging on sponges, other individuals also mine for molluscs in adjacent submerged sandbanks. This leads to the question why individuals select one resource preferentially over another, and whether individuals target a variety of dietary resources across a year, depending on quality availability, similar to other marine and terrestrial omnivores (Werner & Gilliam, 1984; Stamps & Groothuis, 2010).

Our long-term study of loggerhead sea turtles frequenting a foraging site demonstrated the complexity of behaviours and hierarchical structuring that exists. As visual-based technologies continue to emerge allowing us to access and observe the behaviour of elusive animals in ways not previously possible, information on the frequency, intensity and plasticity of interactions under different settings will be revealed. Elucidating how environmental, conspecific and interspecific factors interact could provide new insights on how space is used by sea turtles, and what defines an ‘optimum’ foraging habitat, in terms of biological value and importance for population viability (Rees et al., 2016; Willard, 2013). This information could be applied to inform the implementation and management of protected areas objectively, as well as improve management of captive individuals (Anthony & Blumstein, 2000; Bradbury & Vehrencamp, 2014; Kawazu et al., 2022). In conclusion, our study advances our current understanding of the occurrence and complexity of social interactions between sea turtles in the natural environment.

Author Contributions

Conceptualization: G.S., K.P.; field work: G.S., K.P., C.C., L.W., K.A.K., L.C.D.D.; data analysis: G.S., K.P., C.C., A.S., K.A.K.; home range analysis: L.C.D.D.; writing: led by G.S. with contributions by all authors.

Acknowledgments

This work was funded by Queen Mary University of London, U.K. We thank the handling editor and referees for providing constructive suggestions to improve the manuscript.

Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2022.05.006.

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See Methods for details of sex/maturity discrimination. Code 1 — present in the site, recorded foraging on sponges; code 2 — present in the site, not viewed foraging.

### Appendix

#### Table A1

| Code/name | Turtle no. | Maturity | 2011  | 2012  | 2013  | 2014  | 2015  | 2016  | 2017  | 2018  | 2019  | 2020  | 2021  | Note                  |
|-----------|------------|----------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-----------------------|
| t023, Sotiris | 14         | Adult (male) | 1     | 1     | 2     | 2     | 2     | 2     | 2     |       |       |       |       | Died in 2017 from propeller injury |
| t033, Agisilaos | 11       | Adult (male) | 2     |       |       |       |       |       |       |       |       |       |       |                       |
| t050 | Immature | 2         |       |       |       |       |       |       |       |       |       |       |                       |
| t073, Aglaia | 19         | Immature | 2     | 2     |       |       |       |       |       |       |       |       |       |                       |
| t048, Achille | 1         | Immature (male) | 2 | 2 | 1 | 1 | 1 |       |       |       |       |       |       |                       |
| t109 | Immature (male) | 1         |       |       |       |       |       |       |       |       |       |       |                       |
| t112 | Immature | 2         |       |       |       |       |       |       |       |       |       |       |                       |
| t114 | Immature | 1         |       |       |       |       |       |       |       |       |       |       |                       |
| Green turtle | Immature | 2         |       |       |       |       |       |       |       |       |       |       |                       |
| t115 | Immature | 1         | 1     | 1     | 2     |       |       |       |       |       |       |       |                       |
| t110, Hercules | 6         | Immature | 2     | 1     | 2     |       |       |       |       |       |       |       |       | Died in 2019 from propeller injury |
| t216, Hector | 4         | Immature | 1     | 1     | 1     |       |       |       |       |       |       |       |                       |
| t217, Lucretta | 2         | Immature | 1     | 1     | 1     | 1     |       |       |       |       |       |       |                       |
| t243, George | 3         | Immature | 2     | 1     | 1     | 1     | 1     | 1     | 1     |       |       |       |                       |
| t219 | 5 | Immature | 2 |       |       |       |       |       |       |       |       |       |                       |
| t221, Lola | 10         | Immature | 2     | 1     | 1     |       |       |       |       |       |       |       |                       |
| t222 | Immature | 2         |       |       |       |       |       |       |       |       |       |       |                       |
| t223 | Immature (male) | 2         |       |       |       |       |       |       |       |       |       |       |                       |
| t224 | Adult (female) | 1         |       |       |       |       |       |       |       |       |       |       |                       |
| ‘unnamed male’ | 7         | Immature (male) | 1 |       |       |       |       |       |       |       |       |       |                       |
| t235, Toby | 24         | Immature | 1     | 1     | 1     | 1     |       |       |       |       |       |       |                       |
| t236, Adolfo | 13         | Immature | 1     | 1     | 1     |       |       |       |       |       |       |       |                       |
| t232, Poseidon | 8         | Immature | 1     | 1     | 1     | 1     | 1     | 1     | 1     |       |       |       |                       |
| t233, Orestis | 12        | Immature | 1     | 1     | 1     | 1     | 1     | 1     | 1     |       |       |       | 2021 recording in Gulf of Corinth |
| t324 | 9 | Immature | 2 |       |       |       |       |       |       |       |       |       |                       |
| t325 | Immature | 2         |       |       |       |       |       |       |       |       |       |       |                       |
| t338 | 15         | Immature | 1     | 1     | 1     |       |       |       |       |       |       |       |                       |
| t074 | Immature | 1         |       |       |       |       |       |       |       |       |       |       |                       |
| t346 | Immature (male) | 1         |       |       |       |       |       |       |       |       |       |       |                       |
| t329 | Immature (male) | 1         |       |       |       |       |       |       |       |       |       |       |                       |
| t355 | Immature (male) | 1         |       |       |       |       |       |       |       |       |       |       |                       |
| t397, Keri | 17         | Immature | 1     |       |       |       |       |       |       |       |       |       |                       |
| t398, Elli | 20         | Immature | 1     | 1     | 1     | 1     |       |       |       |       |       |       |                       |
| t399 | Immature (male) | 2         |       |       |       |       |       |       |       |       |       |       |                       |
| t400 | 18         | Immature | 2 |       |       |       |       |       |       |       |       |       |                       |
| G18-01 | Immature | 2         |       |       |       |       |       |       |       |       |       |       |                       |
| G18-03 | Immature | 1 |       |       | 2 |       |       |       |       |       |       |       |                       |
| G18-04, Dias | 22        | Immature | 1     | 1     | 1     |       |       |       |       |       |       |       |                       |
| t441, Diamon | 21        | Immature | 1     |       |       |       |       |       |       |       |       |       |                       |
| t442, Tiny | Immature (male) | 1 |       |       |       |       |       |       |       |       |       |       |                       |
| t522, Marvin | 23        | Immature (male) | 1 | 1 |       |       |       |       |       |       |       |       |                       |
| Pluto | Immature | 1         |       |       |       |       |       |       |       |       |       |       |                       |
**Table A2**
David’s scores calculated for each turtle frequenting the foraging reef at Cameo Islet between 2015 and 2021

| Name   | Turtle no. | 2015  | 2016  | 2017  | 2018  | 2019  | 2020  | 2021  |
|--------|------------|-------|-------|-------|-------|-------|-------|-------|
| Achilles | 1          | 2.25  | 2.33  |       |       |       |       |       |
| Lucretia | 2          | –1.5  | 1.5   | 1.33  | 6.33  |       |       |       |
| George  | 3          | –0.75 | –1.25 | –0.33 | –1.92 | 1.35  | 0.04  | –0.03 |
| Hector  | 4          | –0.25 | 0.5   |       |       |       |       |       |
| t219    | 5          | –0.75 |       |       |       |       |       |       |
| Hercules | 6          | 1.25  | 1.92  |       |       |       |       |       |
| no name | 7          | –0.75 |       |       |       |       |       |       |
| Poseidon| 8          |       |       | –1.58 | –2.1  |       |       |       |
| t324    | 9          |       |       | –1.58 |       |       |       |       |
| Lola    | 10         | –0.5  | 0     | 2     |       |       |       |       |
| Agisalas| 11         |       |       | 1.08  |       |       |       |       |
| Orestis | 12         | –0.5  | –0.83 | –0.42 | –4.1  | –2.04 |       |       |
| Adolfo  | 13         | –1    | –0.5  | –4.42 |       |       |       |       |
| Sotiris | 14         | –0.92 | –0.81 |       |       |       |       |       |
| t338    | 15         | –0.83 |       |       |       |       |       |       |
| t329    | 16         |       | 0.67  |       |       |       |       |       |
| Keri    | 17         | –0.83 |       |       |       |       |       |       |
| t400    | 18         | –0.67 |       |       |       |       |       |       |
| Eli     | 20         | 4.85  | 1.92  | 2.5   |       |       |       |       |
| Diamando| 21         | 0.4   | 0.08  | –1.3  |       |       |       |       |
| Toby    | 24         | 0     | 0.5   |       |       |       |       |       |
| Marvin  | 23         |       |       | 0.5   |       |       |       |       |
| Aglaia  | 19         | –1.68 |       |       |       |       |       |       |
| Dias    | 22         | –0.08 | 0.41  |       |       |       |       |       |

See Methods for details of the calculations used. Turtle no. is the number used for each turtle in the article.

**Table A3**
Analysis of deviance results for the fights from the generalized linear mixed-effects model

|                     | Chisq | df | Pr (>Chisq) |
|---------------------|-------|----|-------------|
| Body size           | 4.17  | 5  | 0.5         |
| Years at site       | 1.93  | 1  | 0.16        |
| Residency (within year) | 4.50  | 1  | **0.03**    |
| Bites by turtle     | 10.88 | 1  | **0.01**    |
| Area                | 2.03  | 1  | 0.15        |
| Fight duration      | 0.34  | 1  | 0.55        |

Significant results are in bold.

**Figure A1.** Relationship between the steepness (corrected for chance) of the David’s score rankings and the number of turtles present in the hierarchy ($F_{1,6} = 5.5$, $r^2 = 0.52$, $P < 0.01$).