

## Article

# Individual Laterality in Ghost Crabs (*Ocypode saratan*) Influences Burrowing Behavior

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**Abstract:** Behavioral handedness is known to enhance an individual's handling capabilities. However, the ecological advantages in brachyuran crustaceans remain unclear, despite the *Ocypode* species having been studied extensively. Thus, in this study, we analyzed the laterality of the endemic Red Sea ghost crab on one beach in Eilat, Israel. We successfully documented the laterality of the large cheliped in 125 crabs; in 60 (48.0%), the right cheliped was larger, and in 64 (51.2%), the left. We also observed temporal segregation between the right- and left-clawed crabs. The right-handed crabs start activity just after sunrise, while left-handed crabs appear ca. 40 min after it. Similarly, temporal segregations were also observed in the evening. The right-clawed crab activity peaked ca. 20 min before sunset, while the left-clawed crabs were active uniformly. Additionally, burrow entrances corresponded to the larger cheliped of the resident individual and is probably a self-defense-related behavior. We conclude that cheliped laterality in *O. saratan* populations should be considered as a bimodal trait, where left- and right-handedness is not under natural selection pressure.

**Keywords:** laterality; claw; ghost crab; burrowing; diurnal; behavior

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## 1. Introduction

Laterality is one of the most visible behavioral–physiological features of organisms, observed in many systematic groups, i.e., both invertebrates and vertebrates. It is suggested that bilateral symmetry represents an evolutionary advantage (e.g., locomotion, sexual selection) that progressively developed in natural populations and can even have a systematic directional bias [1]. The prominent use of either the left or the right limb, for processing or doing specific tasks, was observed in insects [2–4], fish [5–8], reptiles [9], birds [10–13] as well as mammals [14,15]. In the case of the latter, research has focused primarily on humans and primates [16,17]. Nowadays, we know that lateralization influences behavior in animals and is especially pronounced in situations of disturbance or stress (Eastern Grey Kangaroo *Macropus giganteus* [14], Barnacle Goose *Branta leucopsis* and White-fronted Goose *Anser albifrons* [12]).

Behavioral lateralization (handedness), because of asymmetric body traits, is known to enhance an individual's handling capabilities or other functions. For example, in American lobsters (*Homarus americanus*) the left and right claws are individually modified: one as a crusher, and the second as a cutter claw for foraging purposes [18]. However, handedness and its ecological advantages, in brachyuran crustaceans, remain unclear because of the differences between the species. In many of the crustaceans studied to date, the overwhelming majority show handedness in that they have a single enlarged claw (cheliped; [19,20]. In five of the ca. 102 studied species of *Thalassuca* spp., the large claw was predominantly on the right [21], while another study showed that the large claw was equally likely to be either on the left or the right side in most species [22]. Vannini,

M. [23] also found that 92% of *O. ryderi* in Somalia were right-handed. In contrast, the painted ghost crabs (*Ocypode gaudichaudii*) in Costa Rica were found to be predominantly left-handed [24]. So far, there has been no direct research on this aspect, but it is suggested that one larger cheliped is linked to behaviors such as feeding, courtship, territorial defense, or burrow usurpation [25–28].

In fiddler crabs (*Uca mjoebergi*), claws had distinct forces that resulted in different outcomes during fights between conspecific males [29]. In some populations, left-clawed males were a minority and disadvantaged in burrow retainment and when in duels with right-clawed males [30]. Tina, F.W., et al. [31] found that the fighting duration between sparring males was longer if they were homoclaved, but that in burrow retainment fights, residents were more successful than potential usurpers, irrespective of the handedness.

Thus, we conclude that this phenomenon of handedness, in this systematic group, is still puzzling, and no convincing ecological or evolutionary explanation has yet been forwarded. Although other *Ocypode* species have been studied extensively (review in [22,32]), the endemic Red Sea ghost crabs (*O. saratan* Forskål, 1775; RSGC) remain largely unstudied in its geographic range in general [33,34], and in Israel, in particular. Hence, we undertook to study the species at the only beach where the species still exists in Eilat, southern Israel.

The RSGC is endemic to the Red Sea, in the Rift Valley region [35,36]. The species is adapted to a semiterrestrial environment in high-temperature conditions, are gregarious, occupy sandy beaches, and can be identified by the square-shaped carapace and eye stalks with projecting sinuous styliform [34]; both males and females have a single large claw. Ghost crabs are named as such because they are considered to be nocturnal and their pale coloration camouflages them well on the sand [37]. Ghost crabs are organic omnivores and facultative scavengers, whose cleaning of the beaches makes them an important component of the beach-related food webs [38–41].

Earlier studies of the RSGC [33,34] were conducted in Saudi Arabia, Egypt, and Ethiopia; they showed that the Egyptian population was diurnal as compared to the Ethiopian population that was almost entirely nocturnal. Further, although the males in both populations built pyramids near the entrance to their burrows, the Ethiopian population had almost entirely lost their mate-selection function, at least during the moonless nights; vibration signals were prominently used, which the researcher assumed were probably phylogenetically much older [33]. Furthermore, Egyptian males built pyramids at the entrance to their burrows for territory signaling to conspecifics males, for courtship, and mating with females. Courtship is passive wherein males build the sand pyramids but do not actively pursue the females; these are attracted to the pyramids and choose the male by walking into the burrow [33]. Despite the studies of the behavior of this species, the proportion of the positioning of the claws, and their ecological roles, remain obscure. Hence, we studied this endemic, little-studied species at the only beach where the species still exists in Eilat, at the southern tip of Israel.

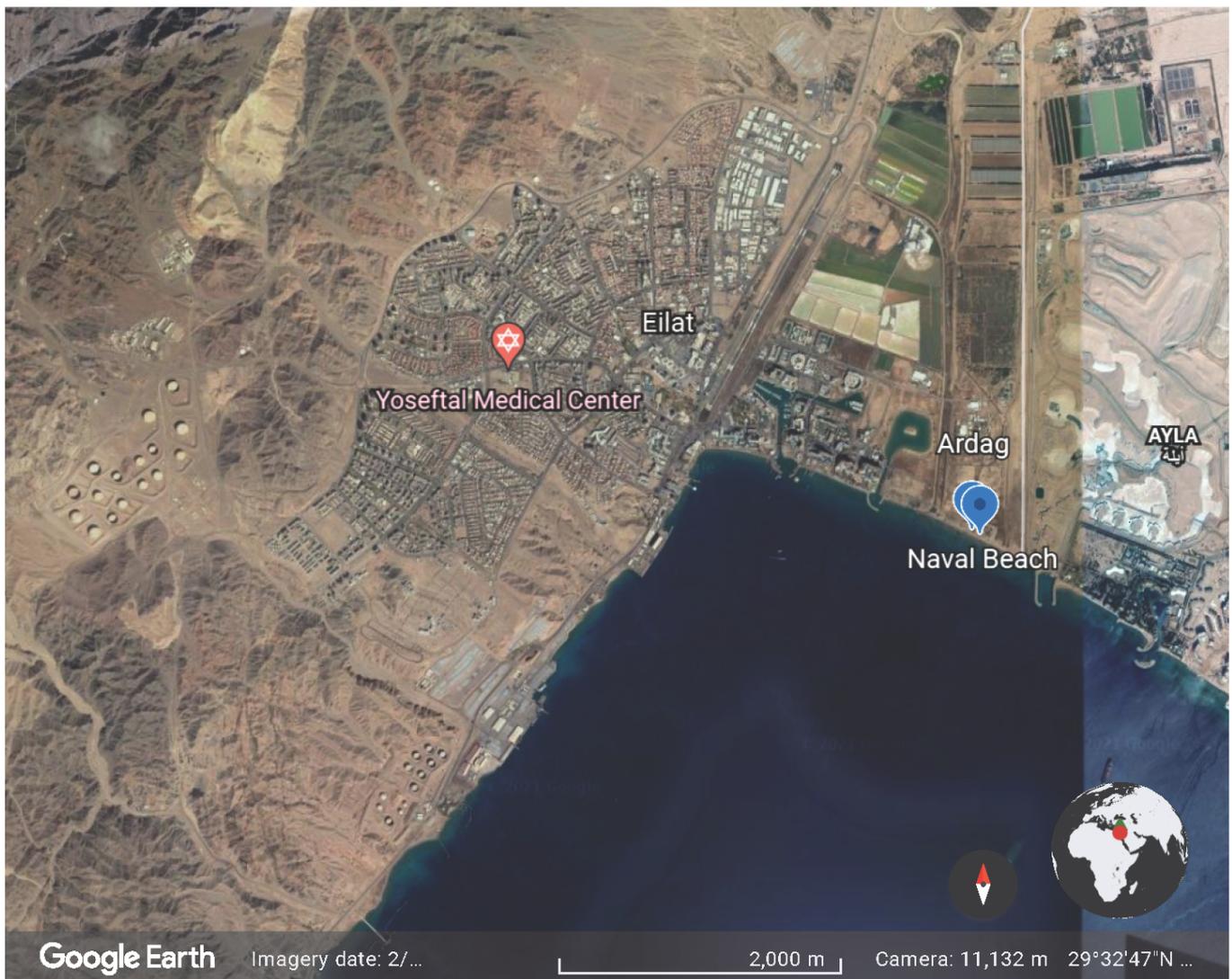
## 2. Methods

### 2.1. Study Area

Our study area is located on the beach in Eilat (29°32′34″ N 34°58′39″ E to 29°32′33″ N 34°58′41″ E; Figure 1), located at the northwestern corner of the eastern arm of the Red Sea. The short section of the beach remains in its original, sandy substrate, while all of the other parts have been covered with gravel to make them more comfortable for beach tourism, making them inhabitable to the RSGC population. None of the individuals are trapped or color-marked for individual identification.

18.8.2021

Google Earth



**Figure 1.** Map showing, encircled, the location of the “Ardag Beach” in Eilat, Israel, where the endemic Red Sea ghost crab (*Ocypode saratan*) can still be seen (Google Maps).

## 2.2. Field Study

The ca. 100 m of sandy beach, along with the 300 m extension eastwards into a military fortification to the east on the border with Jordan, is the last stronghold of the endemic RSGC in Israel. We obtained special permission from the Israeli navy to conduct the study on the undisturbed beach included in the fenced-off area adjacent to the international boundary with Jordan.

At each session, we limited our observations to 2 h. Observations were equally distributed between morning, afternoon, and evening hours. All observations were conducted during March, April and May 2019 and 2020. We conducted a total of 134 h of observation, of which 54 were on the beach of the naval base and 80 on the tourist beach. All observations were conducted with the help of binoculars (10 × 40 Swarovski Optik) to minimize disturbance to the crabs. Observations were also able to be conducted after sunset because the beach of the naval base is lighted by projectors, and the light also reaches the neighboring tourist beach.

At each of the beaches, we sat at a distance of ca. 10 m from the line of burrow entrances, which are distributed uniformly at the high-tide mark, and attempted to identify all the RSGC as they exited their burrows and either foraged on the beach or excavated

sand from within the burrow. After each 2-h session, we observed the same at the adjacent beach. Because it is almost impossible to sex the crabs without catching them, and because the entrance to the burrows of both sexes is very similar [23], and both are lateralized, we collated the data for all the individuals observed during the study.

In crabs for which we successfully established the laterality by noting the larger of the two claws, we also approached their burrow and slid in an elastic strip of 30 mm length to detect the directionality of the entrance to the burrow and the first spiral downwards cf [27,42–44].

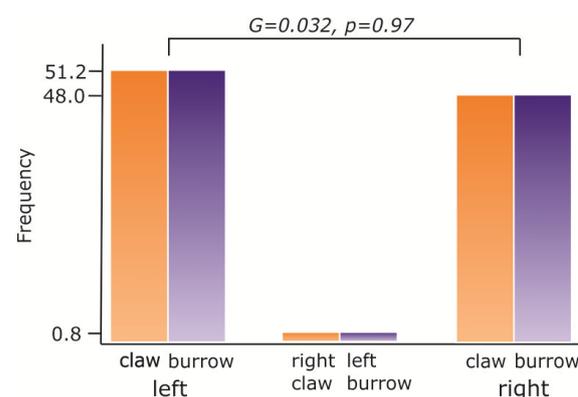
We assumed that even if we, over the research period, resample some of the individuals, the same experiment repeated many times leads to a normal distribution. However, ghost crabs are known to have a fast turnover in burrow occupancy such that the assumption can never really be tested in the field [41,45] unless each of the crabs is individually color marked.

### 2.3. Statistical Analysis

The G-test was used to test the proportion of left and right crabs in the population [46]. We also analyzed by logistic regression [46] the influence time of day on the activity of left- and right-claw crabs to try to understand if the diurnal activity was influenced by lateralization. Additionally, we also employed a *t*-test to test the difference in the average daily activity of crabs with left (0) and right (1) claws. Variation between both groups (0 and 1) in both analyses, i.e., “after sunrise” and “before sunset”, were homogeneous (after sunrise:  $F = 0.89$ ,  $p = 0.81$ ; before sunset:  $F = 2.79$ ,  $p = 0.08$ ). All calculations were performed in R 4.0.2 [47].

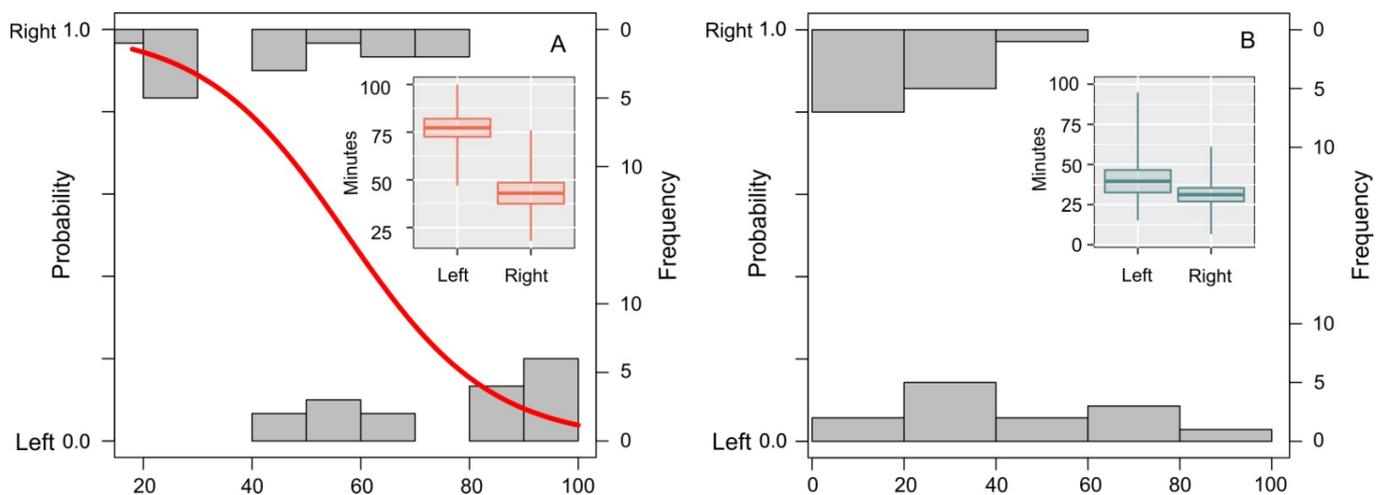
## 3. Results

We successfully documented the laterality of the large cheliped of 125 crabs. Of these 60 (48.0%) the right cheliped was the larger of the two, and in 64 (51.2%), it was the left. The proportion of left and right crabs in the population did not differ significantly ( $G = 0.032$ ,  $p = 0.97$ , Figure 2). Additionally, except for one individual (0.8%) who had a predominant right claw but whose burrow led to the left, all of the rest had burrow entrances that corresponded to the larger cheliped, i.e., those with a larger left cheliped had burrow entrances spiraling to the left and vice versa (Figure 2).



**Figure 2.** The frequency of the larger cheliped in the Red Sea ghost crab (*Ocypode saratan*) and the directionality of the burrow entrance.

We compared the time of day when we observed the activity of the two lateralized groups of RSGC and found that the right-clawed crabs start their diurnal activity just before sunrise (from exactly sunrise to 80 min before sunrise) while the left-clawed crabs start their activity earlier and come out of their burrows ca. from 100 to 40 min before sunrise ( $\beta$ -coefficient  $\pm$  SE =  $2.43 \pm 1.22$ ,  $Z = 1.99$ ,  $p = 0.046$ ,  $R^2 = 0.275$ , Figure 3A). The mean difference between the right- and left-clawed crabs was statistically significant ( $t = 4.71$ ,  $p < 0.0001$ , Figure 3A—internal plot).



**Figure 3.** (A) Activity differentiation between right- and left-clawed crabs 0 to 100 min after sunrise. The right-clawed crabs wake up first, the left-clawed crabs wake up ca. 40 min after sunrise. Boxplot indicates mean (SE, range) differences between right- and left-clawed crabs. (B) Activity differentiation between right- and left-clawed crabs 100 min before sunset. Right-clawed crabs have the highest activity 20 min before sunset, while left-clawed crabs have a constant activity through the evening. Boxplot indicates no differences mean (SE, range) between right- and left-clawed crabs.

In the evening, right-clawed crabs ended activity immediately after sunset, and after 60 min, all individuals entered their burrows, while left-clawed crabs were active uniformly all evening and were observed even 100 min after sunset ( $\beta$ -coefficient  $\pm$  SE =  $-0.58 \pm 0.66$ ,  $Z = -0.85$ ,  $p = 0.378$ ,  $R^2 = 0.06$ , Figure 3B). In this case, we found no significant differences between the right- and left-clawed crabs ( $t = 1.71$ ,  $p = 0.063$ , Figure 3B—internal plot).

#### 4. Discussion

The endemic Red Sea ghost crabs are limited to a very small stretch of the beach in Israel. To understand the ecology of the species, we undertook this study to understand the degree of lateralization within the population. Our results show that the left- or right-handedness in RSGC shows a 1:1 ratio. We did find that the handedness influenced their temporal distribution during the day. However, because we did not study their foraging ecology, we are unable to state whether this also influenced diet. We assume this not to be the case because we have observed all of the individuals breed in the same stretch of the beach, and neighboring burrows can have opposite-handed individuals occupying them. The predators (mostly Indian House Crow *Corvus splendens*) on the beach prey equally on left- and right-handed crabs.

The 1:1 ratio in handedness was previously shown for fiddler crabs (*Uca mjoebergi*) in Australia [28–30]. However, this differs from the *Thalassuca* spp., which is predominantly right-handed [21], and in *U. vocans vomeris*, for which less than 1.4% were left-clawed [30].

In the fiddler crabs, genus *Uca*, all 92 species have an enlarged claw, which is used as a weapon in intra-specific interactions with males or for attraction of females. In 90 of the species, the ratio is equal between left- and right-clawed males. In two species, however, 91–99% of the males are right-clawed [45,48]. It is of interest to note that the researchers found no differences in fighting or other behaviors between the right- and left-clawed individuals. A study of *U. mjoebergi* suggested that handedness created distinct forces and resulted in different outcomes [28,29]. Furthermore, it was also reported that minority left-clawed males were disadvantaged in burrow retainment and appeared to refrain from engaging in duels with right-clawed males, which usually resulted in protracted duels as compared to sparring with homoclaued individuals [30]. Although duels were not observed during our study, we did observe burrow usurpation, and the subject of adaptiveness and ecological advantages raises the question of the lack of claw differentiation in the crustacean populations. A 1:1 ratio in handedness suggests no advantage to any of

the two groups, and yet, habitat segregation and behavioral differences were observed, i.e., different times of activity. If there is an advantage to homoclaved males, then a drift away from the 1:1 ratio would increase, and the handedness that occurs in the lower proportion would be under higher selective pressure and possibly slowly be eliminated from the population. However, this does not appear to be happening in the study population because of segregation. In our study, temporal segregation was observed, and it appears that the two groups avoid intra-specific competition in that the right-handed crabs are active earlier in the morning and their activity declines when the left-handed crabs appear ca. 40 min after sunrise. This temporal segregation was also observed in the evening when the right-clawed crab activity peaked ca. 20 min before sunset, while the left-clawed crabs were active uniformly. Similarly, Seike, K. and Nara, M. [49] demonstrated a different type of segregation. They found habitat segregation in *O. ceratophthalma*, which inhabited the lower dune to foreshore areas, while the *O. sinensis* built their burrows in the dunes of the backshore areas in Japan.

Costa, L.L., et al. [50] thought that the predominantly uniform distribution of the burrows at the high tide mark suggested intra-specific interactions as the driver influencing burrowing behavior and spacing on the beach. Future studies need to question whether the temporal segregation of the RSGC on the beach at Eilat is an artifact of a restricted habitat with unnatural conditions, or a wider phenomenon that needs to be studied at other beaches of the Red Sea that are less frequented by humans. The latter is important because RSGCs subsist in Eilat with constant light during the night and a heavy tourism load during the day. The latter is important because [51], who compared 39 beaches in Brazil, found that beaches with the least human presence had the highest densities of burrows. Similarly, Haque, H. and Choudhury, A. [44] found a positive correlation between the number of people frequenting the beach and the number of crab burrows. Further, Schober, U.M. and Christy, J.H. [52] found that burrowing activity in male painted ghost crabs (*O. gaudichaudhi*) peaked around full and new moons, and these effects may be neutralized by the constant light of the projectors affecting the local population of the RSGC.

Additionally, we found that laterality influenced the directionality of the burrow. Except for one individual, all others dug the initial spiral in the direction of their handedness, i.e., left-clawed individuals to the left and right-clawed to the right. We assume that the single individual was taking refuge in the nearest burrow upon our approach, irrespective of laterality. This finding concurs with that of [33] and that of [23] for *O. ryderi* in Somalia.

RSGCs always exit the burrow with the larger cheliped leading such that we assume this is also self-defense-related behavior (Figure 4). The directional excavation of the burrows probably also facilitates homoclaved females to choose males. This is further substantiated by the fact that [8] found that asymmetry in genitalia was in sync with lateralized mating behavior. This speculation is reflected in another study that found females search for homoclaved partners [32]. Additional study is required to understand the selection pressures on the species and if there is any deviation from the present norm in the future.

Our conclusion is consistent with [24], who underlined in his research of left-handed *Ocypode* crabs in Costa Rica that caution should be exercised in using laterality as the key characteristic for any crustacean species. In our opinion, cheliped laterality in the genus *Ocypode*, and especially in *O. saratan*, should be considered a bimodal trait in the studied population.



**Figure 4.** A right-handed Red Sea ghost crab (*Ocypode saratan*) excavates sand from its burrow. Note that it exits with the larger claw leading while carrying sand in the smaller claw. (Photo: Reuven Yosef).

**Author Contributions:** Conceptualization, R.Y., M.D. and A.S.; data curation, R.Y., M.D., A.S. and J.Z.K.; investigation, R.Y., M.D. and A.S.; methodology, R.Y.; project administration, R.Y.; resources, R.Y.; supervision, R.Y.; validation, R.Y., M.D. and A.S.; writing—original draft, R.Y., M.D., A.S. and J.Z.K.; formal analysis, J.Z.K.; software, J.Z.K.; visualization, J.Z.K. All authors have read and agreed to the published version of the manuscript.

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## References

1. De Lussanet, M.H.E. Opposite asymmetries of face and trunk and of kissing and hugging, as predicted by the axial twist hypothesis. *PeerJ* **2019**, *7*, e7096. [[CrossRef](#)]
2. Anfora, G.; Frasnelli, E.; Maccagnani, B.; Rogers, L.J.; Vallortigara, G. Behavioural and electrophysiological lateralization in a social *Apis mellifera* but not in a non-social *Osmia cornuta* species of bee. *Behav. Brain Res.* **2010**, *206*, 236–239. [[CrossRef](#)] [[PubMed](#)]
3. Frasnelli, E.; Vallortigara, G.; Rogers, L.J. Left-right asymmetries of behaviour and nervous system in invertebrates. *Neurosci. Biobehav. Rev.* **2012**, *36*, 1273–1291. [[CrossRef](#)]
4. Benelli, G.; Romano, D. Looking for the right mate: What do we really know on the courtship and mating of *Lucilia sericata* (Meigen)? *Acta Tropica* **2019**, *189*, 145–153. [[CrossRef](#)]
5. Bisazza, A.; Cantalupo, C.; Robins, A.; Rogers, L.J.; Vallortigara, G. Right-pawedness in toads. *Nature* **1996**, *379*, 408. [[CrossRef](#)]
6. Bisazza, A.; Facchin, L.; Vallortigara, G. Heritability of lateralization in fish: Concordance of right–left asymmetry between parents and offspring. *Neuropsychologia* **2000**, *38*, 907–912. [[CrossRef](#)]
7. Stancher, G.; Sovrano, V.A.; Vallortigara, G. Motor asymmetries in fishes, amphibians, and reptiles. *Prog. Brain Res.* **2018**, *238*, 33–56.

8. Torres-Dowdall, J.; Rometsch, S.J.; Gastón, A.; Goyenola, G.; Meyer, A. Asymmetry in genitalia is in sync with lateralized mating behavior but not with the lateralization of other behaviors. *Curr. Zool.* **2020**, *66*, 71–81. [[CrossRef](#)]
9. Hews, D.K.; Castellano, M.; Hara, E. Aggression in females is also lateralized: left-eye bias during aggressive courtship rejection in lizards. *Anim. Behav.* **2004**, *68*, 1201–1207. [[CrossRef](#)]
10. Yosef, R.; Gindi, C.; Sukenik, N. Footedness in Steppe Buzzard (*Buteo vulpinus*). *Behav. Process.* **2019**, *158*, 113–116. [[CrossRef](#)]
11. Hugo, C.; Henry, L.; George, I.; Schedir, M.; Martine, H. Lateralization of social signal brain processing correlates with the degree of social integration in a songbird. *Sci. Rep.* **2020**, *10*, 14093.
12. Galuret, S.; Lumineau, S.; Pouzol, D.; George, I. Mothering influences domestic chick's laterality. *Anim. Behav.* **2020**, *159*, 69–79. [[CrossRef](#)]
13. Zaynagutdinova, E.; Karenina, K.; Giljov, A. Lateralization in monogamous pairs: Wild geese prefer to keep their partner in the left hemifield except when disturbed. *Curr. Zool.* **2021**, *67*, 419–429. [[CrossRef](#)]
14. Sinisalchi, M.; Padalino, B.; Lusito, R.; Quaranta, A. Is the left forelimb preference indicative of a stressful situation in horses? *Behav. Proc.* **2014**, *107*, 61–67. [[CrossRef](#)] [[PubMed](#)]
15. Karenina, K.; Giljov, A.; Ingram, J.; Rowntree, V.J.; Malashichev, Y. Lateralization of mother—Infant interactions in a diverse range of mammal species. *Nat. Ecol. Evol.* **2017**, *1*, 1–4. [[CrossRef](#)]
16. Hauser, M.D.; Akre, K. Asymmetries in the timing of facial and vocal expressions by rhesus monkeys: Implications for hemispheric specialisation. *Anim. Behav.* **2001**, *61*, 391–400. [[CrossRef](#)]
17. Leliveld, L.M.C.; Scheumann, M.; Zimmermann, E. Effects of caller characteristics on auditory laterality in an early primate *Microcebus murinus*. *PLoS ONE* **2010**, *5*, e9031. [[CrossRef](#)] [[PubMed](#)]
18. Govind, C.K. Asymmetry in lobster claws. *Am. Sci.* **1989**, *77*, 468–474.
19. Hamilton, P.V.; Nishimoto, R.T.; Halusky, J.G. Cheliped laterality in *Callinectes sapidus* (Crustacea: Portunidae). *Biol. Bull. Woods Hole* **1976**, *150*, 393–401. [[CrossRef](#)] [[PubMed](#)]
20. Vermeij, G.J. Patterns in claw size: The geography of crushing. *Systematic. Zool.* **1977**, *26*, 138–151. [[CrossRef](#)]
21. Rosenberg, M.S. The systematics and taxonomy of fiddler crabs: A phylogeny of the genus *Uca*. *J. Crustacean Biol.* **2001**, *21*, 839–869. [[CrossRef](#)]
22. Crane, J. *Fiddler Crabs of the World*; (Ocypodidae: Genus *Uca*); Princeton University Press: Princetown, NJ, USA, 1975.
23. Vannini, M. Researches on the coast of Somalia. The shore and dune of Sar Uanle. 27. Burrows and digging behavior in *Ocypode* and other crabs (*Crustacean Brachyura*). *Monite. Zool. Ital. N. S. Ecol. Monog.* **1980**, *13*, 11–44.
24. Trott, T.J. The Prevalence of Left-handedness in the Painted Ghost Crab *Ocypode gaudichaudii* H. Milne Edwards & Lucas (Decapoda: Brachyura: Ocypodidae). *Crustaceana* **1987**, *52*, 213–215. [[CrossRef](#)]
25. Ng, P.K.L.; Tan, L.W.H. 'Right handedness' in the heterochelous calappoid and xanthoid crabs—Suggestion for a functional advantage. *Crustaceana* **1985**, *49*, 98–100.
26. Morrell, L.J.; Backwell, P.R.Y.; Metcalfe, N.B. Fighting in fiddler crabs *Uca mjoebergi*: What determines duration? *Anim. Behav.* **2005**, *70*, 653–662. [[CrossRef](#)]
27. Chan, B.K.K.; Chan, K.T.Y.; Leung, P.C.M. Burrow architecture of the Ghost Crab *Ocypode ceratophthalma* on a sandy shore in Hong Kong. *Hydrobiologia* **2006**, *560*, 43–49. [[CrossRef](#)]
28. Perez, D.M.; Rosenberg, M.S.; Pie, M.R. The evolution of waving displays in fiddler crabs (*Uca* spp., Crustacea: Ocypodidae). *Biol. J. Linn. Soc.* **2012**, *106*, 307–315. [[CrossRef](#)]
29. Perez, D.M.; Heatwole, S.J.; Morell, L.J.; Blackwell, P.R.Y. Handedness in fiddler crab fights. *Anim. Behav.* **2015**, *110*, 99–104. [[CrossRef](#)]
30. Backwell, P.R.Y.; Matsumasa, M.; Double, M.; Roberts, A.; Murai, M.; Keogh, J.S.; Jennions, M.D. What are the consequences of being left-clawed in a predominantly right-clawed fiddler crab? *Proc. R. Soc. B* **2007**, *274*, 2723–2729. [[CrossRef](#)] [[PubMed](#)]
31. Tina, F.W.; Jaroensutasinee, M.; Jaroensutasinee, K. Body size, resident status, handedness and claw originality in *Uca rosea* (Tweedie, 1937) male fights. *Crustaceana* **2016**, *89*, 1687–1700. [[CrossRef](#)]
32. Tiralongo, F.; Messina, G.; Marino, S.; Bellomo, S.; Vanadia, A.; Borzì, L.; Tibullo, D.; Di Stefano, A.; Lombardo, B.M. Abundance, distribution and ecology of the tufted ghost crab *Ocypode cursor* (Linnaeus, 1758) (Crustacea: Ocypodidae) from a recently colonized urban sandy beach, and new records from Sicily (central Mediterranean Sea). *J. Sea Res.* **2020**, *156*, 101832. [[CrossRef](#)]
33. Von Linsenmair, K.E. Konstruktion und Signalfunktion de Sandpyramide der Reiterkrabbe *Ocypode saratan* Forsk. (Decapoda Brachyura Ocypodidae). Ph.D. Thesis, Aus dem Zoologischen Institut der Universität Frankfurt, Frankfurt, Germany, 1967; p. 54.
34. Eshky, A.A. Aspects of the Ecology, Behaviour and Physiology of the Ghostcrab (*Ocypode Saratan*). Ph.D. Thesis, University of Glasgow, Glasgow, Scotland, UK, 1985; p. 451.
35. Fishelson, L. Ecology and distribution of the benthic fauna in the shallow waters of the Red Sea. *Mar. Biol.* **1971**, *10*, 113–133. [[CrossRef](#)]
36. Fishelson, L. Population ecology and biology of *Dotilla sulcata* (Crustacea, Ocypodidae) typical for sandy beaches of the Red Sea. In *Sandy Beaches as Ecosystems*; McLachlan, A., Erasmus, T., Eds.; Dr W. Junk Publishers: The Hague, The Netherlands, 1983; pp. 643–654.
37. Karleskint, G.; Turner, R.K.; Small, J. Intertidal communities. In *Introduction to Marine Biology*, 3rd ed.; Cengage Learning: Boston, MA, USA, 2009.

38. Wolcott, T.G. Ecological role of ghost crabs, *Ocypode quadrata* (Fabricius) on an ocean beach: Scavengers or predators? *J. Exp. Mar. Biol. Ecol.* **1978**, *31*, 67–82. [[CrossRef](#)]
39. Trott, T.J. Gustatory responses of ghost crab *Ocypode quadrata* to seawater extracts and chemical fractions of natural stimuli. *J. Chem. Ecol.* **1999**, *25*, 375–388. [[CrossRef](#)]
40. Marco, A.; Da Graça, J.; García-Cerdá, R.; Abella, E.; Freitas, R. Patterns and intensity of ghost crab predation on the nests of an important endangered loggerhead turtle population. *J. Exp. Mar. Biol. Ecol.* **2015**, *468*, 74–82. [[CrossRef](#)]
41. Deidun, A.; Crocetta, F.; Sciberras, A.; Sciberras, J.; Insacco, G.; Zava, B. The protected taxon *Ocypode cursor* (Linnaeus, 1758) (Crustacea: Decapoda: Ocypodidae)—Documenting its well-established presence in the central Mediterranean. *Eur. Zool. J.* **2017**, *84*, 96–103. [[CrossRef](#)]
42. Nye, P.A. Burrowing and burying by the crab *Macrophthalmus hirtipes*. *N. Z. J. Mar. Freshw. Res.* **1974**, *8*, 243–254. [[CrossRef](#)]
43. Seike, K.; Nara, M. Occurrence of bioglyphs on *Ocypode* crab burrows in a modern sandy beach and its palaeoenvironmental implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2007**, *252*, 458–463. [[CrossRef](#)]
44. Haque, H.; Choudhury, A. Ecology and behavior of the ghost crab *Ocypode macrocerca* Edwards 1834 occurring in the sandy beaches of Sagar Island, Sunderbans. *Int. J. Eng. Sci. Invent.* **2014**, *3*, 38–43.
45. Pratt, A.E.; McLain, D.K.; Lathrop, G.R. The assessment game in sand fiddler crab contests for breeding burrows. *Anim. Behav.* **2003**, *65*, 945–955. [[CrossRef](#)]
46. Sokal, R.R.; Rohlf, F.J. *Biometry*, 3rd ed.; W. H. Freeman: New York, NY, USA, 1995.
47. R Development Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2010.
48. Jennions, M.D.; Backwell, P.R.Y. Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biol. J. Linn. Soc.* **1996**, *57*, 293–306. [[CrossRef](#)]
49. Seike, K.; Nara, M. Burrow morphologies of the ghost crabs *Ocypode ceratophthalma* and *O. sinensis* in foreshore, backshore, and dune environments of a sandy beach in Japan. *J. Geol. Soc. Jpn.* **2008**, *114*, 591–596. [[CrossRef](#)]
50. Costa, L.L.; Soares-Gomes, A.; Zalmon, I.R. Burrow occupation rates and spatial distribution within habitat of the ghost crab *Ocypode quadrata* (Fabricius, 1787): Implications for impact assessments. *Reg. Stud. Mar. Sci.* **2021**, *44*, 101699. [[CrossRef](#)]
51. De Souza, G.N.; Oliviera, C.A.G.; Tardem, A.S.; Soares-Gomes, A. Counting and measuring ghost crab burrows as a way to assess the environmental quality of beaches. *Ocean Coast. Manag.* **2017**, *140*, 1–10. [[CrossRef](#)]
52. Schober, U.M.; Christy, J.H. Sand disposal of the painted ghost crab *Ocypode gaudichaudii* (Decapoda: Ocypodidae): A possible role in courtship. *Mar. Biol.* **1993**, *116*, 53–60. [[CrossRef](#)]