



Juvenile Aggression, Wounding, and Behavioral Signaling in Galápagos Giant Tortoises (*Chelonoidis*)

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Turtles—including freshwater turtles, marine turtles, and tortoises—demonstrate a range of agonistic behaviours related to male-male competition for mates, female harassment during mating, and resource competition (Auffenberg 1977; Lindeman 1999; Moldowan et al. 2020; Schofield et al. 2022). Due to their large size, charisma, and relative ease of observation, tortoises in the genus *Chelonoidis* have been the frequent subjects of behavioral observations and studies, particularly in captivity (Freeland et al. 2020; Le Balle et al. 2021; Fieschi-Méric et al. 2022; Madile Hjelt et al. 2024). Among Galápagos giant tortoises, antagonism is particularly well documented in adults of saddleback taxa (Fritts 1983; Schafer and Krekorian 1983; Nieuwolt 1989) but less is known for domed taxa. We herein describe agonistic behaviour among wild juvenile Eastern Santa Cruz Giant Tortoises (*Chelonoidis donfaustoi*), a domed taxon. We also discuss wounding in the context of conspecific behavioral signalling, and provide morphological descriptions of head and neck coloration among species of Galápagos giant tortoises.

Methods

Monitoring the ecology and reproductive biology of several species of Galápagos giant tortoises has been ongoing since 2009 via the Galápagos Tortoise Movement Ecology Program (GTMEP).

To date, studies of the GTMEP have involved four species across three islands: Western Santa Cruz Giant Tortoise (*C. porteri*) and Eastern Santa Cruz Giant Tortoise (*Chelonoidis donfaustoi*) on Santa Cruz Island, Española Giant Tortoise (*C. hoodensis*) on Española Island, and the Alcedo Volcano Giant Tortoise (*C. vandenburghi*) of the Alcedo Volcano, Isabela Island. During 2023–2025, detailed reproductive monitoring of free-living *C. donfaustoi* (Donovan et al., in press) provided opportunities for behavioral observations. During fieldwork, we opportunistically recorded observations of juvenile aggression and wounding. PDM also conducted observational stud-

ies of juveniles of several species — *C. donfaustoi*, *C. hoodensis*, Santiago Giant Tortoise (*C. darwini*), and individuals of Floreana Giant Tortoise (*C. niger*) ancestry — at the Fausto Llerena Tortoise Breeding Center, Puerto Ayora, Santa Cruz Island, Galápagos, and noted body sizes, morphology, and wounding.

Results

Observation 1.—At 0734 h local time (UTC–6) on 22 September 2023, we encountered two combative juvenile *C. donfaustoi* in the vicinity of Cerro Fatal on eastern Santa Cruz Island, Galápagos (0.6, -90.3; WGS 84). We observed interactions from about 15 m for approximately 10 min, of which 6 min and 50 sec were recorded (Video S1: <https://youtu.be/TCJuJY9yyIc>). The smaller juvenile, measuring 40 cm in curved midline carapace length (CCL; Method E in Iverson and Lewis 2018), asserted itself as the aggressor by confronting, biting, and trailing the larger juvenile (47 cm CCL). The video recordings documented approximately 31 biting attempts by the smaller individual, of which at least 19 bites (61%) contacted the larger individual. Of landed bites, 13 were delivered to the left forelimb and six to the left hindlimb of the larger individual. The larger individual did not contact the small individual during any of five bite attempts. In addition, the smaller individual displaced the larger individual approximately one meter during a bout of pushing (beginning 1:10 of Video S1). The two individuals repeatedly elevated their bodies, fully extended their necks, hissed, and gaped throughout the observation period. The smaller juvenile emerged as the apparent victor in all of the brief contests, often landing bites, physically displacing, and forcing retreat of the larger individual. Observations ceased when the tortoises moved into vegetation. White scarring around the jowls of both juveniles was visible at a distance and was confirmed by subsequent field observations (Fig. 1A shows the larger, subordinate juvenile). Two Galápagos



Figure 1. Wounding on Eastern Santa Cruz Giant Tortoises (*Chelonoidis donfaustoi*): Wild juvenile (47 cm CCL; also seen as subordinate juvenile in Video S1) (A); free-living juvenile recently released from the Fausto Llerena Tortoise Breeding Center, Santa Cruz Island (42 cm CCL) (B); and wild adult female (94 cm CCL) (C). Note scabbing and heavy callousing on the jowl of the captive-raised juvenile (B); although the left side of the head and neck are shown, wounding also occurs on the right side of the head, tympanum, upper throat, and occasionally eyelid areas. Photographs by P.D. Moldowan.

Mockingbirds (*Mimus parvulus*) were foraging in the immediate area during the observation period.

Observation 2.—At 0748 h local time (UTC–6) on 29 February 2024, we encountered an adult female (94 cm CCL) and juvenile (44 cm CCL) *C. donfaustoi* in the vicinity of Cerro Fatal (as above). We observed the interaction from approximately 5 m. The juvenile initially was positioned immediately in front of and facing the stationary adult, and out of the line-of-sight of observers. A video totaling 4 min and 49 sec recorded behavioral interactions (Video S2: <https://youtu.be/j-92Yt7ycaU>). At the onset of the observation, the juvenile moved to the anterior left side of the adult, raised its neck and head, gaped, and attempted to bite the adult (0:00–0:05). In response to repeated bites and biting attempts by the juvenile (e.g., 0:04, 0:12, 0:46, 1:33), the adult demonstrated several behaviors, including defensive recoiling (e.g., 0:12 and 1:33), hissing (e.g., 1:32, 4:42), gaping or attempted biting (0:57), and elevating its body (0:16 and 1:34). The juvenile was exploratory (starting 1:48), repeatedly walking along the flanks of the adult and investigating its fore- and hindlimbs with an outstretched neck, apparently smelling (2:05, 2:52–3:40) and nipping the posterior carapace of the adult (3:14) before returning to the anterior of the adult to bite (3:50). During the observation period, the juvenile landed at least three bites (0:46, 1:33, 3:50). One landed bite to the soft tissue between the left forelimb and axillary region (3:50) caused the adult to begin quickly walking away. The juvenile continued to pursue the adult and, upon catching up after approximately 50 m, the juvenile resumed biting at the tail and hindlimbs of the adult (4:40). Overall, the juvenile landed several bites, physically displaced, and forced retreat of the much larger adult. Observations concluded at 0800 h at which time the tortoises began to move into thicker vegetation and were held for body size measurements.

Discussion

Aggression in Galápagos tortoises.—The agonistic observations reported herein are notable for two reasons: aggression was exhibited by juveniles and by members of a domed Galápagos giant tortoise taxon. Agonistic interactions in wild Galápagos giant tortoises are known, but largely restricted to adults and among individuals of the saddleback taxa (particularly Pinzón Giant Tortoises, *C. duncanensis*, and *C. hoodensis*). Agonistic encounters among saddleback taxa involve individuals maximizing vertical extension of the limbs and neck, gaping, and, if conflict escalates, striking and biting the head and neck of opponents (Fritts 1983; Schafer and Krekorian 1983; Nieuwolt 1989). Victors of these contests, typically considered the dominant individuals, are those that extend their head highest (Fritts 1983; Schafer and Krekorian 1983; Nieuwolt 1989). Among wild adult *C. duncanensis*, agonistic encounters occurred frequently with larger individuals with greater neck extensions displacing subordinates, gaining access to preferred foods, and spending more time engaged in mating behavior (Nieuwolt 1989).

Compared to the physical confrontations described for saddleback taxa, the relatively few interactions described among adult *C. porteri* (domed) involved elevated shell posturing, head-raised displays, and gaping (Rodhouse et al. 1975; S. Blake, pers. obs. in Blake et al. 2021). Unlike many other tortoises, Galápagos giant tortoises do not ram opponents nor are they equipped with sexually dimorphic gular scutes that are used as weapons and flipping appendages (e.g., as in *Astrochelys yniphora*, *Chersina angulata*, *Gopherus* spp.; Auffenberg 1966; Branch 1984; Mandimbihasina and Currylow 2014).

Observations of juvenile *Chelonoidis* demonstrating aggression are infrequent and discussion about the possible importance of these interactions for social behavior and organization is lacking. Captive-bred juvenile *C. dun-*

canensis released onto Pinzón Island engaged in agonistic behavior within minutes of release (MacFarland and Reeder 1975). Blake (pers. obs. in Blake et al. 2021) documented an extended agonistic encounter between two juvenile *C. donfaustoi*. Over 45 minutes, a slightly larger juvenile persistently and aggressively pursued a smaller individual biting at the head, neck, and hindlimbs. The smaller juvenile attempted escape, but never demonstrated retaliatory aggression. No obvious competition for resources was evident among these juveniles and the agonistic interaction was interpreted as dominance. Despite little research, complex social behavior and organization are expected in giant tortoises and other chelonians, juveniles included (Blake et al. 2021). Considering their longevity, remarkable memory (Wilkinson et al. 2007; Gutnick et al. 2020), range in personalities (Carlson and Tetzlaff 2020; Reed et al. 2023), dominance hierarchies

(Evans and Quaranta 1951; Schafer and Krekorian 1983; Fieschi-Méric et al. 2022), and comparatively high densities in the wild prior to human exploitation (Gibbs and Goldspiel 2021), giant tortoise are fascinating subjects for sociobiological studies.

Conspecific wounding in wild and captive Galápagos giant tortoises.—Injuries caused by conspecifics have been used to infer cryptic behavior and social dynamics in turtles and other wildlife (e.g., Foott 1970; Hiruki et al. 1993; Keevil et al. 2017). Wounding has not been recorded in hatchling and yearling tortoises in nature or captivity (PDM, pers. obs.). However, juvenile Galápagos giant tortoises measuring 20–50 cm CCL (~3–5 or more years of age) exhibit scabbing, scarring, and callousing on the jowls, neck, and occasionally eyelids in nature (Fig. 1A) and captivity (Fig. 1B), suggesting that conspecific aggression increases with age and/or size. Such



Figure 2. Coloration on the head and neck of wild Galápagos giant tortoises: Española Giant Tortoise (*Chelonoidis hoodensis*), a saddleback taxon (A); Alcedo Volcano Giant Tortoise (*C. vandenburghi*), a domed taxon (B); and Western Santa Cruz Giant Tortoise (*C. porteri*), a domed taxon (C). See also Fig. 1C for an adult Eastern Santa Cruz Giant Tortoise (*C. donfaustoi*), a domed taxon. Photographs by P.D. Moldowan.

injuries were common among hundreds of inspected juveniles of several taxa, including *C. donfaustoi* (domed), *C. darwini* (saddleback), *C. hoodensis* (saddleback), and individuals of *C. niger* ancestry (saddleback), maintained in the Fausto Llerena Tortoise Breeding Center (PDM, pers. obs.). Scarring along the jowls, neck, and throat occurs regularly in wild adults of both sexes of at least *C. donfaustoi* (domed), *C. hoodensis* (saddleback), *C. porteri* (domed), and *C. vandenburghi* (domed) (Fig. 1C, Fig. 2B–C) (PDM, pers. obs.), demonstrating that agonistic biting is not limited to captive settings.

Coloration, signaling, and wounding.—Saddleback taxa of Galápagos giant tortoises demonstrate obvious yellow coloration of the beak, chin, and neck (Van Denburgh 1914; Pritchard 1996) (Fig. 2A). This yellow coloration is more common in males than females and might function in signaling and intensifying aggressive behavior (Schafer and Kjekshus 1983; Fritts 1984, cited in Chiari 2021; Chiari 2021). Pritchard (1996: 38) remarked that “the extent of the unpigmented area on the face and throat, while generally more developed in the saddleback forms, definitely varies with age.” Fritts (2001, cited in Chiari 2021) commented that yellow and white unpigmented blotches occur along the jaws of older individuals. Despite the attention given to head and throat coloration in saddleback taxa, no proposed explanations in the literature explain the more subtle unpigmented coloration present around the jowls and tympani of domed tortoises (Fig. 1, Fig. 2B–C). Whereas the yellow coloration of saddleback taxa appears to be an inherent and naturally occurring pigment, perhaps mediated by genetics and hormones and evolved for conspecific signaling, the white, unpigmented coloration observed in domed taxa appears to be the result of acquired epidermal tissue wear and scarring. A likely explanation for the wounding/scarring is conspecific aggression. Tortoises in the genus *Chelonoidis* have notched beaks with bicuspid or tricuspid tomiodonts, tooth-like cusps of the premaxillaries and beaks (Moldowan et al. 2016). From a biomechanical standpoint, this tomiodont arrangement can generate high bite force and low levels of work, strain, and deformation on the bite material (Anderson and LaBarbera 2008; Moldowan et al. 2016). This beak morphology is effective for cutting tough, malleable materials (Anderson and LaBarbera 2008), such as plant stems and leaves, and is expected to cause laceration during biting. Similar conspecific wounding has been observed in freshwater turtle taxa with bicuspid tomiodonts, such as *Chrysemys* and *Pseudemys* (Moldowan 2020). Alternatively, or in addition, the wear and scarring on the head and neck regions of domed tortoises could result from abrasive materials, such as grit, caught in folds of skin when the head is retracted. However, the absence of such abrasions elsewhere on the bodies of tortoises where soil collects (soft tissue of the limbs and inguinal regions) suggests that scarring on their head and neck is not simply caused by environmental

wear. If wounding is related to conspecific aggression, future studies involving Galápagos giant tortoises might consider evaluating scarring as a metric of social rank, mating behavior, and reproductive desirability, among other cryptic aspects of biology, as has been done in other taxa (Foott 1970; Hiruki et al. 1993; Scott et al. 2005; Keevil et al. 2017; Moldowan et al. 2020; Lanyon et al. 2021).

Overall, behavioral observations and wounding suggest that Galápagos giant tortoises demonstrate agonistic interactions as juveniles and support ideas of dominance and social structuring in wild giant tortoise populations. Blake et al. (2021) highlighted that behavioral interactions and social organization of *Chelonoidis* across age classes and taxa remain open for exploration and are sure to be interesting. Detailed observational studies alongside modern advances in wildlife monitoring and tracking technologies makes studies of socio-biology of giant tortoises an exciting possibility.

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