



# Dramatic Fighting by Male Cuttlefish for a Female Mate

Justine J. Allen, Derya Akkaynak, Alexandra K. Schnell, Roger T. Hanlon

## ► To cite this version:

Justine J. Allen, Derya Akkaynak, Alexandra K. Schnell, Roger T. Hanlon. Dramatic Fighting by Male Cuttlefish for a Female Mate. *The American Naturalist*, 2017, 190 (1), pp.144-151. 10.1086/692009 . hal-01521970

**HAL Id: hal-01521970**

**<https://univ-rennes.hal.science/hal-01521970v1>**

Submitted on 12 May 2017

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# Dramatic Fighting by Male Cuttlefish for a Female Mate

Justine J. Allen,<sup>1,\*</sup> Derya Akkaynak,<sup>2</sup> Alexandra K. Schnell,<sup>3</sup> and Roger T. Hanlon<sup>1,4</sup>

1. Brown University, Providence, Rhode Island; 2. Interuniversity Institute for Marine Sciences, Eilat, Israel; and Department of Marine Technologies, University of Haifa, Israel; 3. Groupe Mémoire et Plasticité comportementale, Université de Caen Normandie, Caen, France; 4. Marine Biological Laboratory, Woods Hole, Massachusetts

Submitted August 23, 2016; Accepted February 10, 2017; Electronically published May 2, 2017

**ABSTRACT:** Male cuttlefish compete for females with a repertoire of visually dramatic behaviors. Laboratory experiments have explored this system in *Sepia officinalis*, but corroborative field data have eluded collection attempts by many researchers. While scuba diving in Turkey, we fortuitously filmed an intense sequence of consort/intruder behaviors in which the consort lost and then regained his female mate from the intruder. These agonistic bouts escalated in stages, leading to fast dramatic expression of the elaborate intense zebra display and culminating in biting and inking as the intruder male attempted a forced copulation of the female. When analyzed in the context of game theory, the patterns of fighting behavior were more consistent with mutual assessment than self-assessment of fighting ability. Additional observations of these behaviors in nature are needed to conclusively determine which models best represent conflict resolution, but our field observations agree with laboratory findings and provide a valuable perspective.

**Keywords:** *Sepia officinalis*, agonistic, cephalopod, behavior, sexual selection, evolutionary game theory.

## Introduction

Sexual selection is a key feature of animal life histories, and extraordinarily diverse reproductive tactics have evolved to achieve reproductive success (Andersson 1994; Oliveira et al. 2008). Coleoid cephalopods are short-lived mollusks that are well known for their unique system of changeable coloration used for signaling and camouflage (Hanlon and Messenger 1996; Darmaillacq et al. 2014). They can alter their appearance in as little as half a second due to direct neural control of millions of pigmented chromatophore organs in the skin (Hill and Solandt 1935; Hanlon 2007). The common European cuttlefish, *Sepia officinalis* L., has complex courtship and mating behaviors, as noted first by Aristotle (1910, translation) and Tinbergen (1939). It is one of few cephalopod species whose reproductive tactics have been tested and

characterized through laboratory experiments. However, field observations of sexual selection processes under natural conditions have never been accomplished despite considerable attempts.

*Sepia officinalis* is renowned for its visual capabilities, rapid adaptive camouflage, learning, and memory, and thus it is perhaps surprising that this species of cuttlefish appears to lack social recognition, including the capability to identify individual mates or rivals (Boal 1996, 2006; Palmer et al. 2006). Instead, sexual recognition is rather primitive. Although there is some evidence that females can recognize other females using visual cues (Palmer et al. 2006), cuttlefish typically identify the gender of their conspecifics using a signal-response system. Sexually mature male cuttlefish rapidly exhibit the intense zebra display to other cuttlefish (Hanlon and Messenger 1988). Animals that respond by displaying this pattern in return are assumed by the signaling cuttlefish to be male; animals that fail to mirror it are considered female and might be subjected to attempted copulations, regardless of sex (Messenger 1970). Male cuttlefish presented with a mirror also reliably showed the intense zebra display (37 of 48 presentations; Adamo and Hanlon 1996), emphasizing the role of visual stimuli as well as the lack of self-recognition.

Male cuttlefish compete vigorously for female mates. Larger males win most fights; for example, larger males forced smaller males to retreat in 11 of 14 laboratory trials (Adamo and Hanlon 1996). When sexually mature male cuttlefish fight, key components of the intense zebra display, such as the darkness of one male's face, can predict whether their behavior will escalate to a violent agonistic encounter (Adamo and Hanlon 1996). Initially, each animal adopts a body pattern composed of light and dark zebra stripes. Next, one or both animals extends his fourth arm (the only sexually dimorphic character) toward the other male. They also produce a dark ring around the eye, sometimes with a unilaterally dilated pupil. When both males maintain a dark face (many brown chromatophores expanded), the encounter is likely to escalate to grappling or biting. Interestingly, Adamo and Hanlon (1996) found

\* Corresponding author; e-mail: justine\_allen@brown.edu.

**ORCID:** Allen, <http://orcid.org/0000-0001-9974-4226>; Akkaynak, <http://orcid.org/0000-0002-6269-4795>; Hanlon, <http://orcid.org/0000-0003-0004-5674>.

Am. Nat. 2017. Vol. 190, pp. 000–000. © 2017 by The University of Chicago. 0003-0147/2017/190001-57200\$15.00. All rights reserved.

DOI: 10.1086/692009

that males initially reluctant to fight (i.e., they did not display a dark face to another male) were motivated in subsequent encounters to engage in bouts with other males if they had mated with a female in the interim.

Although laboratory experiments are useful in teasing apart the details of complex behavioral sequences during sexual selection, observing these behaviors in nature with wild, unrestrained animals is required for complete understanding. Here, we report the first field observation of mate guarding and male-male aggression in the common European cuttlefish, *S. officinalis*. The results are discussed in relation to game theory models to describe the patterns of fighting behavior between the male opponents.

There are two types of theoretical models applied to animal contests; each differs in its assumptions about how opponents gather information about fighting ability, termed resource-holding potential (RHP; Arnott and Elwood 2009). The first type, termed self-assessment strategies, assumes that opponents evaluate their own RHP but fail to assess their opponent's RHP (e.g., energetic war of attrition model [E-WOA; Payne and Pagel 1996]; cumulative assessment model [CAM; Payne 1998]). The second type, termed mutual assessment strategies, is analyzed through the sequential assessment model (SAM), which assumes that opponents evaluate their own RHP relative to their opponent's RHP (Enquist and Leimar 1983). These models differ in three key predictions. First, the E-WOA model posits that opponents match energy expenditure by matching frequency, duration, and intensity of behaviors for the majority of the contest (Payne 1998). By contrast, both the CAM and the SAM hypothesize that opponents do not match energy expenditure, and thus behaviors are typically unmatched (Payne 1998). Second, there are differences among the models in the pattern of escalation within the contests. Both self-assessment strategies (E-WOA and CAM) assume that opponents differ in rates of escalation within phases (i.e., periods characterized by behaviors of similar aggressive intensity). On the other hand, mutual-assessment strategies (SAM) assume that opponents do not differ in rates of escalation; rather, they progress through a series of successive phases, which is thought to provide accurate information about the RHP difference between contestants. Third, the most distinguishing feature involves the relationship between contest duration and RHP and demonstrates whether RHP assessment is based on the opponent's relative RHP or their own RHP thresholds. The E-WOA predicts that decisions to withdraw are based on self-imposed energetic costs, whereas the CAM predicts that decisions to withdraw are based on a combination of self-imposed costs and costs inflicted by the opponent (i.e., injuries). In both of these models, contests end when the losing opponent reaches his threshold, thus contest duration is expected to be a function of the weaker individual's RHP (but see Taylor and Elwood 2003). By contrast, the SAM predicts that de-

cisions to withdraw are based on the RHP of the loser relative to the winner, and thus contest duration is expected to be a function of RHP asymmetry between the losing and winning opponents. Given the rarity of our field encounter, our sample size is small and does not meet the minimum number of samples required to conduct unequivocal statistical analyses to test the key predictions of game theory. However, it does allow us to describe these natural behaviors in the context of game theory and to provide a conceptual framework to determine self-assessment or mutual assessment strategies of fighting in this species.

## Methods

Cuttlefish were observed in the Aegean Sea near Çeşmealtı, Turkey, in a shallow nearshore habitat of 3 m depth. Photographs were taken with a Canon EOS 1Ds Mark II digital SLR camera in a Subal underwater housing (Subal, Vienna, Austria), and video was recorded with a FlipCam (Irvine, CA) compact camera in an underwater housing. Field footage was analyzed using playback software (Apple Macintosh, Final Cut Pro X 10.0.8) to record mate guarding and fighting behaviors. The durations of behaviors were measured to the nearest second using the timestamps in the digital image and video metadata. The start of an agonistic bout was defined as the point of engagement between the two males, when the receiver responds to (i.e., looks at, moves toward) the signaler. We defined the end of an agonistic bout to occur when one male retreated from the interaction for at least 10 s. Cuttlefish were identified by their size and scars and by unique patterns of white zebra bands (Boal 1996).

To examine whether the males matched energy expenditure during the agonistic interaction, we recorded the frequency of a series of agonistic behaviors. These included dark and light banding (i.e., zebra banding), unilateral extension of the fourth arm, dark eye ring, dilated pupil, dark face, inking, swiping, grappling, lunging, biting, and rolling. We classified these behaviors into three levels of aggressive intensity, consistent with previous research (Adamo and Hanlon 1996). Weak zebra banding, fourth arm extension, and dark eye ring are typically exhibited during the early stages of a bout in the absence of physical aggression, thus these were classified as low-level aggressive behaviors. Strong zebra banding, inking, dark eye ring with a dilated pupil, and dark face are typically exhibited during later stages of a bout and are often associated with mantle pushing, thus these were classified as medium-level aggressive behaviors. Behaviors that involved attempted physical aggression or physical combat, such as swiping, grappling, lunging, biting, and rolling, were classified as high-level aggressive behaviors.

To compare the intensity of zebra banding shown by each male, seven RAW digital photos were selected for

analysis. The linearity of the sensor response of the camera (and therefore the RAW images) was verified for an earlier study (Akkaynak et al. 2014). Image analysis was done using ImageJ software (ver. 1.8.0-101), and only images with a view of at least one male's mantle were used. The region of the image comprising a male's mantle was selected manually, the RGB values of the enclosed region were measured (gray scale: 0 = black and 255 = white), and the standard deviation of those values was recorded. A standard deviation less than 10 was classified as weak zebra banding, and a standard deviation greater than 10 was classified as strong zebra banding.

We visualized the pattern of escalation between the winning male and the losing male by examining the progression of behaviors and the duration of each bout. Owing to a small sample size, we did not conduct statistical analyses on these data, and instead we present descriptive data to illustrate the patterns of fighting behavior between the two male opponents.

### Results

A lone, mature female cuttlefish was filmed as she swam slowly across a sandy shallow environment with patches of seagrass. She had white scars on her right mantle, mantle tip, and left third arm, indicative of intraspecific aggression. A male cuttlefish (male 1) quickly approached her and settled on the sand next to a clump of algae approximately 2 m from the female. The female slowly moved a few meters away, but male 1 remained stationary and camouflaged for 362 s (fig. 1A). Suddenly, male 1 darted toward the female, grabbed her with his arms, and they mated in a head-to-head position (239 s; fig. 1B). No courtship behavior was observed. Apparent flushing of the female's buccal area (where sperm from previous matings are stored; Hanlon et al. 1999) began approximately 39 s into copulation and continued intermittently for 110 s. Our video data did not reveal whether a sperm packet was transferred to the female.

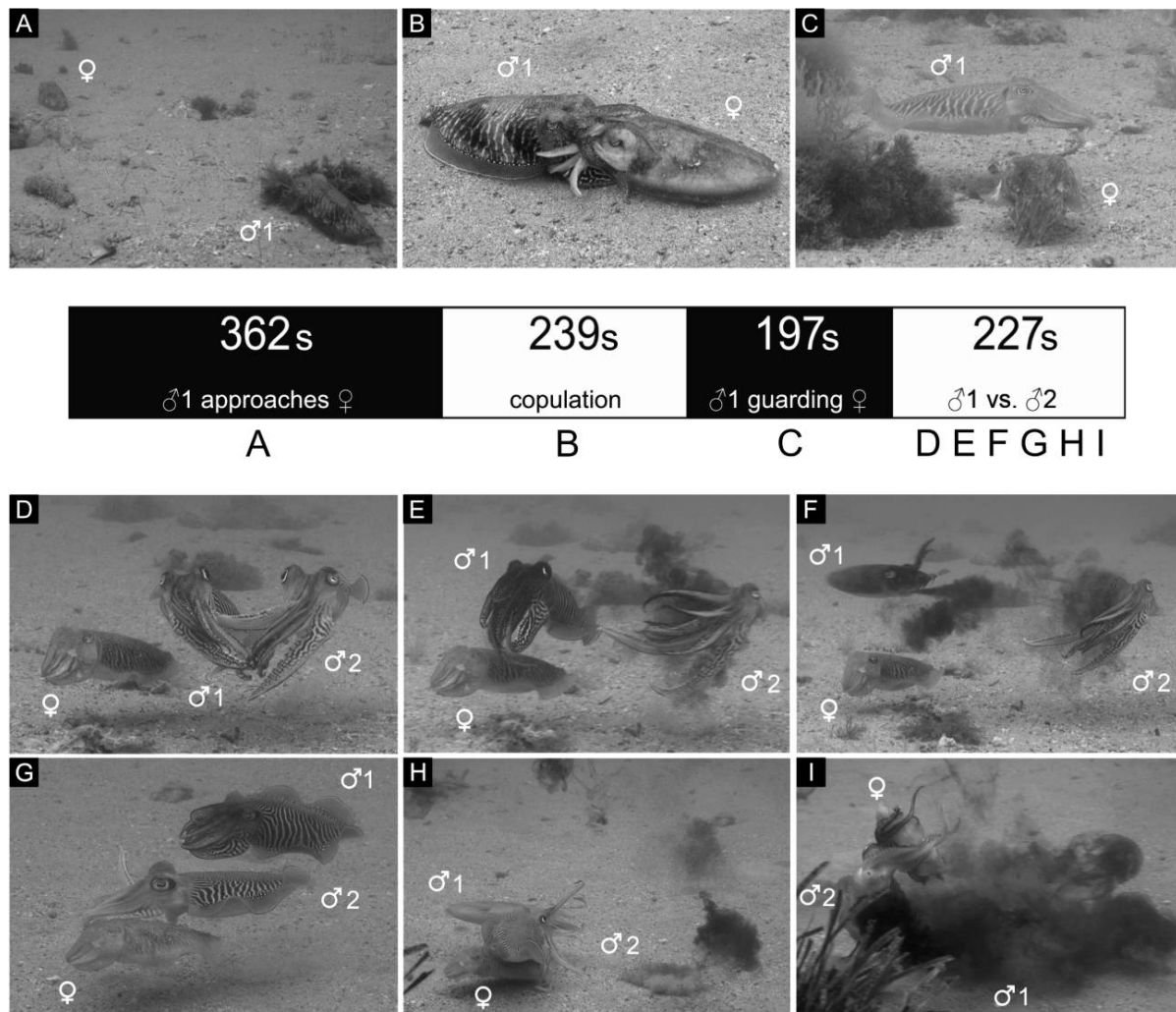
Following copulation, the male 1 (consort male) guarded the female for 197 s (fig. 1C); he swam closely alongside her and at her speed (Hanlon and Messenger 1996). Suddenly, an intruder male (male 2; approximately the same size as male 1) quickly approached the pair and unilaterally displayed an extended fourth arm and a dilated pupil toward male 1 (fig. 1D). Male 1 responded with extended fourth arm and dark face and then both produced high-contrast black-and-white zebra bands in their skin; collectively, these constitute the intense zebra display (figs. 1D, 3A). Seven seconds later, the consort rapidly darkened his whole body pattern (a sign of alarm; Hanlon and Messenger 1988; fig. 1E) and then inked and jetted away, having lost the bout (fig. 1F). The former intruder (male 2) paired with and guarded the female, but 78 s later, male 1 approached again and challenged male 2 with a dark face and zebra banding that led

to another intensive agonistic bout (fig. 1G). During the next 10 s, male 1 inked and jetted around the pair in a dynamic set of displays (fig. 1H). Male 2 then grabbed the female's mantle in a mating attempt (which appeared to be a forced copulation) just as male 1 grabbed male 2's posterior mantle, and all three animals were briefly entangled: male 1 holding the posterior mantle of male 2 and male 2 holding the mantle of the female (fig. 1I). The female broke free and jetted away while male 1 violently twisted male 2 in three corkscrew motions (like a barrel roll) for an additional 9 s while both animals inked profusely. Male 2 broke free, and male 1 chased him several meters while the female remained high in the water column. Male 1 returned and paired again with the female, and they were video-recorded swimming calmly for approximately 6 min more. Male 2 did not return before the scuba dive was terminated due to low air levels. Overall, the male-male aggressive interactions occurred over 227 s, with three aggressive bouts lasting 14 s, 25 s, and 47 s, respectively. Male 2 (intruder) won bouts 1 and 2, while male 1 (consort) won bout 3. Supplementary video sequences and color photographs are available at <https://doi.org/10.7301/Z0PR7SX4>; sequences of behaviors shown by each male and an illustration of the skin patterns, arm posture, and pupil dilation are presented in figure 2.

Details of unilateral signaling and posturing and subsequent stepwise escalation were evident in these video and photograph sequences (figs. 1–3). The initial aggressive behavior involved the extension of the fourth arm toward the other male (fig. 2B); both the left (fig. 3A) and right (fig. 3B) fourth arms were extended depending on the position of the challenger. A slightly higher level of aggression was indicated when the zebra bandings on the mantle and arms were expressed unilaterally with high contrast (cf. low contrast of male 1 vs. high contrast [fig. 2B] of male 2 in fig. 3A, 3C). The eye components differed as well: a dark ring around the eye indicated low-level aggression, while a ring around the eye plus widely dilated pupil indicated medium-level aggression (figs. 2B, 3C). Three times during these bouts the eventual winner showed at least one dilated pupil and the loser did not. Full escalation of the visual display involved both animals showing the intense zebra pattern combined with an arching and tilting of the body so that the whole dorsal side of the cuttlefish was visually evident to the opponent. Fullest escalation was manifest by grappling and biting.

Speeds of change from one dynamic skin patterning signal to the next are shown below the labels in figure 2B. Each of these visual signals represents a single neurophysiological component that is controlled directly from the brain. Thus, they can each be expressed in the skin patterning in an eye blink: 270–730 ms. Combining several of the component visual signals into simultaneous expression of a whole body pattern such as the intense zebra display occurred in 530 ms.





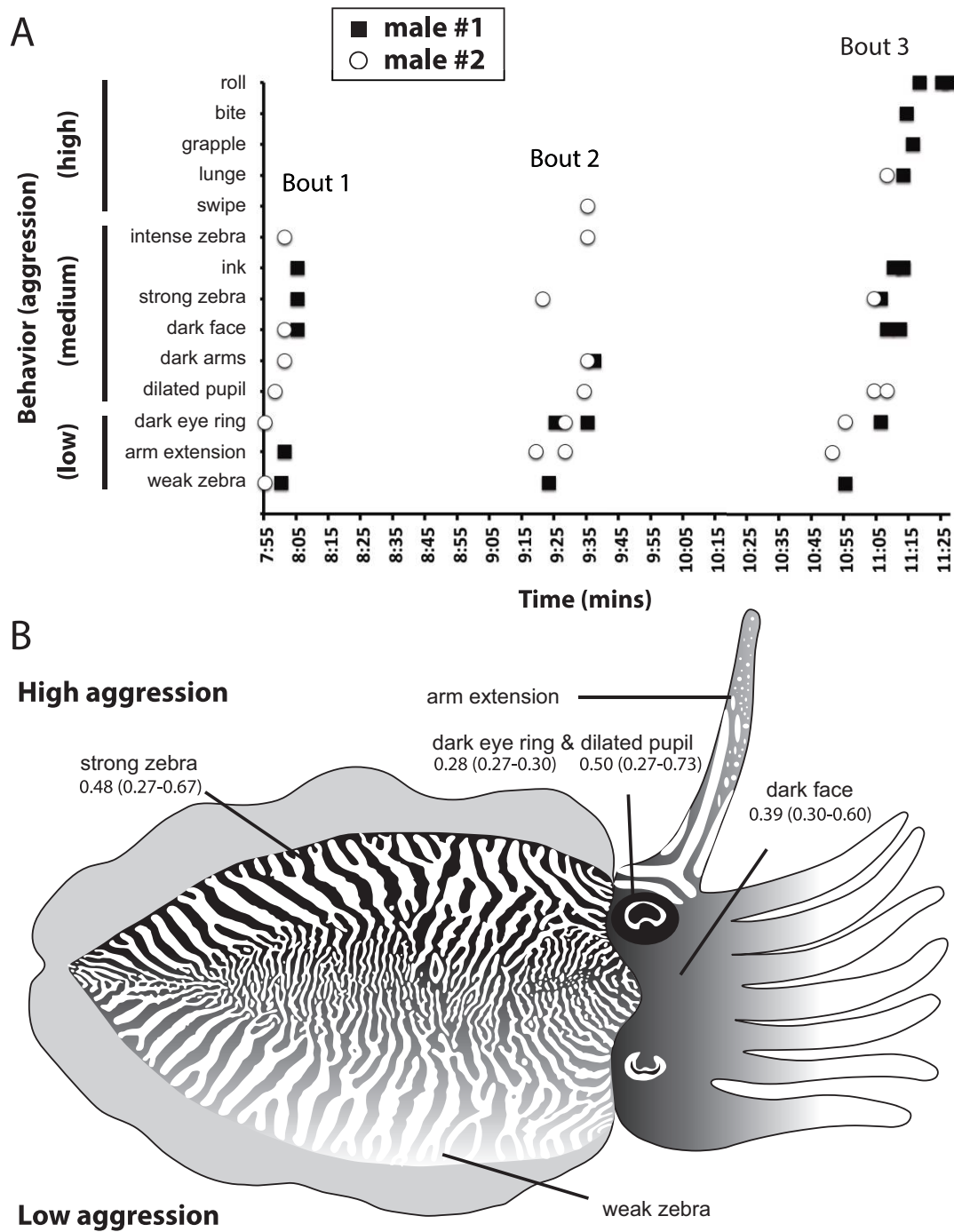
**Figure 1:** Two male cuttlefish (consort, male 1; intruder, male 2) competing for a female in the Turkish Aegean Sea. *A*, The consort male approached the female. *B*, The consort male copulated with the female for about 4 min. *C*, The consort male remained in proximity to the female for more than 2 min. *D*, The consort male and the female were approached by male 2, and they began chromatic and postural signaling. The consort male showed a dark face during an intense zebra display (*E*) and then inked and jetted away (*F*). *G*, The original consort male later approached male 2, who was now the consort, and engaged in another agonistic bout. *H*, Male 1 darts in very closely to male 2 in an attempt to take over consortship once again. *I*, Attached to each other, the males tossed the trio in several barrel rolls; the female broke loose and jetted toward the surface; and the males rolled a few additional turns before separating and swimming away.

The winning and losing males performed similar frequency of low-level aggressive behaviors throughout the bouts (fig. 2A). However, the winning male (male 2 in bouts 1 and 2, male 1 in bout 3) performed more medium-level and high-level aggressive behaviors than the losing male (fig. 2A). For the three bouts, the rate of escalation appeared to follow a pattern of successive progression (fig. 2A). Additionally, the zebra stripe contrast measurements showed that once a male signaled strong zebra banding, he usually continued to signal at this level of aggression. This pattern

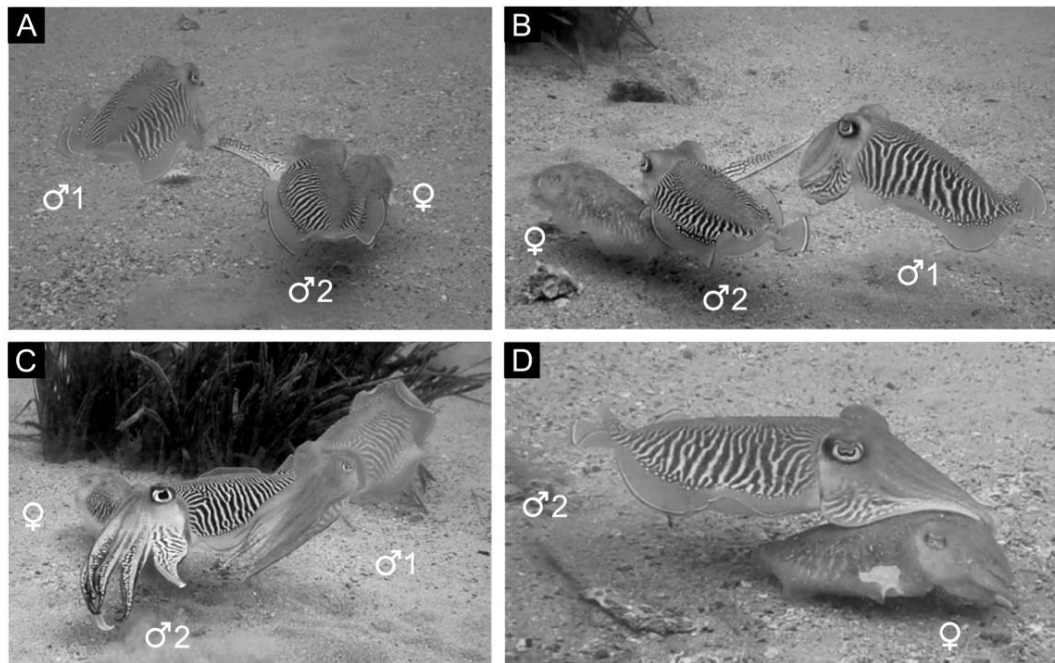
of escalation suggests that male *Sepia officinalis* use sequential signaling during contests.

### Discussion

In these agonistic encounters, observed under natural conditions, the overall intensity and violence of the fights was surprising because extensive laboratory observations to date have not reported so much fast jetting, inking, grappling, and savage biting. Mate guarding by both males



**Figure 2:** Escalation of aggressive behaviors during three consecutive male-male bouts. *A*, Fourteen behaviors categorized as low-, medium-, and high-level aggression. Behaviors shown by male 1 (original consort) are indicated with black boxes, and those shown by male 2 (intruder) are indicated with open circles. *B*, Illustration of various aggressive patterning and postural agonistic behaviors; the average speed of appearance (range) in seconds is presented below the signal labels.



**Figure 3:** Unilateral chromatic and postural signaling during mate guarding. *A*, Male 2, intruder and temporary consort, extending his left arm and expressing intense zebra patterning on the left side of his body. *B*, When the challenger moves to his right side, male 2 extends his right arm; note that the challenging male has a dark eye ring but his pupil is not dilated. *C*, The dilated pupil by consort male 2, who has all arms extended toward the challenging male. *D*, Male 2 temporarily paired with the female and gently touching her during mate guarding (rival male 1 was 1 m above them).

was intense. Male 1 mated with the female before any competition occurred, and the mating duration (3.98 min) was similar to laboratory observations (2.5–7 min; Hanlon et al. 1999; Palmer et al. 2006). The female was not receptive to the intruder male 2; we could not determine whether that copulation attempt failed due to female choice or because it occurred in the midst of intense agonistic bouts. Both Boal (1996) and Adamo et al. (2000) found that dominant consort males won more fights and obtained more copulations; our brief observations do not confirm this but tend to suggest the same. There were no indications of any form of courtship between the female and either male, which also agrees with laboratory observations (Boal 1996, 1997; Boal et al. 1999; Hanlon et al. 1999; Adamo et al. 2000). Moreover, the female did not pay attention to the fights and even wandered away twice; this also seems typical of this species (Boal 1997) as well as the giant Australian cuttlefish, *Sepia apama* (Hall and Hanlon 2002). Boal (1997) found that female choice in *Sepia officinalis* was not based on winners of fights as much as it was on apparent chemical cues: the male that had mated most recently was the choice of females in that laboratory study.

The structure of the agonistic bouts was not consistent with the self-assessment model (E-WOA). Our results indi-

cate that the winning and losing males did not match behaviors throughout each bout, suggesting that the opponents did not match the energy expenditure assumption of the E-WOA model. Although low-level aggressive behaviors were similar between the winning and losing males, the winning male appeared to perform medium-level and high-level aggressive behaviors at higher frequencies (fig. 2A). A recent study on the giant Australian cuttlefish *S. apama* reported similar structural patterns during male-male contests. Male *S. apama* matched behaviors during low-level aggression; however, winners outperformed losers during high-level aggression (Schnell et al. 2015).

Likewise, the pattern of escalation within the agonistic bouts was not consistent with the predictions of the self-assessment models (E-WOA and CAM). These models predict that escalation can occur within phases and that high-level aggressive behaviors can occur throughout the bout (Mesterton-Gibbons et al. 1996). Instead, our results show that the males performed a generalized sequence of escalation, typically beginning with low-level aggressive behaviors and escalating to high-level aggressive behaviors, showing the following stepwise progression: weak zebra banding, fourth arm extension, dark eye ring > dark eye ring with dilated pupil, dark face, strong zebra banding, inking > intense



zebra display > swiping, grappling > biting, rolling. This pattern of escalation is supported by previous laboratory experiments, whereby staged agonistic bouts between *S. officinalis* appear to follow a distinct stepwise sequence (Adamo and Hanlon 1996). Two previous studies on different cephalopod species, squid *Doryteuthis (Loligo) plei* (DiMarco and Hanlon 1997; van Staaden et al. 2011) and cuttlefish *S. apama* (Schnell et al. 2015, 2016), have also demonstrated stepwise progression during male-male contests. Moreover, the study on *S. apama* revealed that escalation did not occur within contest phases (Schnell et al. 2015). While our data tend to suggest the same pattern, we were unable to verify whether escalation within phases is indeed absent in fighting male *S. officinalis* due to our small sample size in this serendipitous field event. Additional field observations are needed to validate this pattern, analyze the interactions among aggressive behaviors, and measure contest outcome and duration.

A noteworthy uniqueness in cephalopod signaling is the ultrafast skin patterning changes (fig. 2B) that can produce a wide range of expression from subtle to dramatic, enabling the animal more diversity in appearance than other animals. The behavioral significance of such refinement is largely unknown, but it is worth recalling that cephalopod vision is excellent, and they may be modifying their intra-specific signaling more than we can interpret at this time.

Overall, more field studies are needed to learn the variations of reproductive tactics of both males and females. No known spawning aggregations exist for *S. officinalis*, and it seems that such observations will be fortuitous because only small groups of this species have ever been observed, even in spawning season (early spring), along European coastlines and the Mediterranean Sea. The best-known and field-studied cuttlefish species is *S. apama* because they aggregate annually in large numbers in shallow, nearshore water and are comparatively easy to record and sample (Norman et al. 1999; Hall and Hanlon 2002; Naud et al. 2004, 2005; Hanlon et al. 2005). The ultimate evidence for successful fighting and consortship is genetic reproductive success, and field studies on *S. apama* (Norman et al. 1999; Hall and Hanlon 2002; Naud et al. 2004, 2005; Hanlon et al. 2005) using DNA fingerprinting have been the most successful in indicating this in cephalopods. Perhaps future field and laboratory studies of *S. officinalis* and other cephalopods will illuminate our understanding of these key behaviors for sexual selection processes. For example, is the rate of the escalation of aggression consistent among bouts? In how many bouts will rivals engage before the aggression becomes physical? Does the physical size of the competitors influence the frequency and aggression of bouts? In other words, are males that are more similar in size—and, presumably, fighting ability—more willing to engage in a series of increasing intensity than mismatched males? These and many other questions must be tested in naturalistic condi-

tions and observed in the wild before we can truly understand the aggressive behaviors employed in the competition for mates by this species.

### Acknowledgments

S. Akkaynak was a gracious host in Turkey, and E. Yellin was an invaluable diving partner; we are thankful for their unflagging support. Thanks to H. Singh for lending us the FlipCam and its housing and to A. Creamer and H. Lappen for help with data archiving. This work was improved by the constructive comments of two anonymous reviewers; we appreciate the time and effort they applied to their critiques. J.J.A. was supported by a National Defense Science and Engineering Graduate Fellowship and a National Science Foundation Graduate Research Fellowship; A.K.S. was supported by a postdoctoral study grant from the Fyssen Foundation; R.T.H. was funded partly by the Sholley Foundation and supported by Office of Naval Research grant N0001406-1-0202.

### Literature Cited

- Adamo, S. A., W. M. Brown, A. J. King, D. L. Mather, J. A. Mather, K. L. Shoemaker, and J. B. Wood. 2000. Agonistic and reproductive behaviours of the cuttlefish *Sepia officinalis* in a semi-natural environment. *Journal of Molluscan Studies* 66:417–419.
- Adamo, S. A., and R. T. Hanlon. 1996. Do cuttlefish (Cephalopoda) signal their intentions to conspecifics during agonistic encounters? *Animal Behaviour* 52:73–81.
- Akkaynak, D., T. Treibitz, B. Xiao, U. A. Gürkan, J. J. Allen, U. Demirci, and R. T. Hanlon. 2014. Use of commercial off-the-shelf digital cameras for scientific data acquisition and scene-specific color calibration. *Journal of the Optical Society of America A* 31:312–321.
- Andersson, M. B. 1994. Sexual selection: monographs in behavior and ecology. Princeton University Press, Princeton, NJ.
- Aristotle. 1910. The works of Aristotle. Clarendon Press, Oxford.
- Arnott, G., and R. W. Elwood. 2009. Probing aggressive motivation in a cichlid fish. *Biology Letters* 5:762–764.
- Boal, J. G. 1996. Absence of social recognition in laboratory-reared cuttlefish, *Sepia officinalis* L (Mollusca: Cephalopoda). *Animal Behaviour* 52:529–537.
- . 1997. Female choice of males in cuttlefish (Mollusca: Cephalopoda). *Behaviour* 134:975–988.
- . 2006. Social recognition: a top down view of cephalopod behaviour. *Vie Et Milieu—Life and Environment* 56:69–79.
- Boal, J. G., R. A. Hylton, S. A. Gonzalez, and R. T. Hanlon. 1999. Effects of crowding on the social behavior of cuttlefish (*Sepia officinalis*). *Contemporary Topics in Laboratory Animal Science* 38:49–55.
- Darmaillacq, A.-S., L. Dickel, and J. Mather. 2014. Cephalopod cognition. Cambridge University Press, Cambridge.
- DiMarco, F. P., and R. T. Hanlon. 1997. Agonistic behavior in the squid *Loligo plei* (Loliginidae, Teuthoidea): fighting tactics and the effects of size and resource value. *Ethology* 103:89–108.
- Enquist, M., and O. Leimar. 1983. Evolution of fighting behavior: decision rules and assessment of relative strength. *Journal of Theoretical Biology* 102:387–410.
- Hall, K. C., and R. T. Hanlon. 2002. Principal features of the mating system of a large spawning aggregation of the giant Australian



- cuttlefish *Sepia apama* (Mollusca: Cephalopoda). *Marine Biology* 140:533–545.
- Hanlon, R. 2007. Cephalopod dynamic camouflage. *Current Biology* 17:R400–R404.
- Hanlon, R. T., S. A. Ament, and H. Gabr. 1999. Behavioral aspects of sperm competition in cuttlefish, *Sepia officinalis* (Sepioidea: Cephalopoda). *Marine Biology* 134:719–728.
- Hanlon, R. T., and J. B. Messenger. 1988. Adaptive coloration in young cuttlefish (*Sepia officinalis* L.)—the morphology and development of body patterns and their relation to behavior. *Philosophical Transactions of the Royal Society B* 320:437–487.
- . 1996. *Cephalopod behaviour*. Cambridge University Press, New York.
- Hanlon, R. T., M. J. Naud, P. W. Shaw, and J. N. Havenhand. 2005. Transient sexual mimicry leads to fertilization. *Nature* 433:212.
- Hill, A. V., and D. Y. Solandt. 1935. Myograms from the chromatophores of *Sepia*. *Journal of Physiology* 83:13–14.
- Messenger, J. B. 1970. Optomotor responses and nystagmus in intact, blinded and statocystless cuttlefish (*Sepia officinalis* L.). *Journal of Experimental Biology* 53:789–796.
- Mesterton-Gibbons, M., J. H. Marden, and L. A. Dugatkin. 1996. On wars of attrition without assessment. *Journal of Theoretical Biology* 181:65–83.
- Naud, M. J., R. T. Hanlon, K. C. Hall, P. W. Shaw, and J. N. Havenhand. 2004. Behavioural and genetic assessment of reproductive success in a spawning aggregation of the Australian giant cuttlefish, *Sepia apama*. *Animal Behaviour* 67:1043–1050.
- Naud, M. J., P. W. Shaw, R. T. Hanlon, and J. N. Havenhand. 2005. Evidence for biased use of sperm sources in wild female giant cuttlefish (*Sepia apama*). *Proceedings of the Royal Society B* 272:1047–1051.
- Norman, M. D., J. Finn, and T. Tregenza. 1999. Female impersonation as an alternative reproductive strategy in giant cuttlefish. *Proceedings of the Royal Society B* 266:1347–1349.
- Oliveira, R. F., M. Taborsky, and H. J. Brockmann, eds. 2008. *Alternative reproductive tactics: an integrative approach*. Variation: MyiLibrary, New York.
- Palmer, M. E., M. R. Calve, and S. A. Adamo. 2006. Response of female cuttlefish *Sepia officinalis* (Cephalopoda) to mirrors and conspecifics: evidence for signaling in female cuttlefish. *Animal Cognition* 9:151–155.
- Payne, R. J. H. 1998. Gradually escalating fights and displays: the cumulative assessment model. *Animal Behaviour* 56:651–662.
- Payne, R. J. H., and M. Pagel. 1996. Escalation and time costs in displays of endurance. *Journal of Theoretical Biology* 183:185–193.
- Schnell, A. K., C. L. Smith, R. T. Hanlon, K. C. Hall, and R. Harcourt. 2016. Cuttlefish perform multiple agonistic displays to communicate a hierarchy of threats. *Behavioral Ecology and Sociobiology* 70:1643–1655.
- Schnell, A. K., C. L. Smith, R. T. Hanlon, and R. Harcourt. 2015. Giant Australian cuttlefish use mutual assessment to resolve male-male contests. *Animal Behaviour* 107:31–40.
- Taylor, P. W., and R. W. Elwood. 2003. The mismeasure of animal contests. *Animal Behaviour* 65:1195–1202.
- Tinbergen, L. 1939. Zur Fortpflanzungsethologie von *Sepia officinalis* L. *Archives Néerlandaises de Zoologie* 3:323–364.
- van Staaden, M. J., W. A. Searcy, and R. T. Hanlon. 2011. Signaling aggression. *Advances in Genetics* 75:23–49.

Natural History Editor: Mark A. McPeck



Justine J. Allen and one of the cuttlefish. Photo credit: Derya Akkaynak.