

fossils. After I started working on the origin of birds, I realized that the traditional paleontological approach was not sufficient for understanding bird origins. To get a reasonably complete picture of the evolution of avian features, we need not only data from fossils but also insights from other disciplines. So I started working with the developmental biologists Cheng-Ming Chuong of the University of Southern California and Susan Mackem of the National Cancer Institute, the comparative genomicist Guojie Zhang of the University of Copenhagen and the China National GeneBank, and the biomechanist Robert Dudley of the University of California at Berkeley, among others, in order to understand how feathers and wings evolved and how avian flight originated. This approach turned out to be fruitful, and I've co-authored several papers with these collaborators in different disciplines. I've also been communicating a lot with Huanming Yang of the Beijing Genomics Institute — one of China's leading genetics scientists — and we've even co-organized academic symposiums to promote crosstalk between paleontology and neontology. The history of evolutionary biology is all about integrating an ever-growing number of disciplines into evolutionary studies, and I believe that this trend will continue into the future.

What do you think about post-publication peer review of papers?

Post-publication peer review is a great idea and definitely benefits the scientific community. I believe that almost every scientist has at some point wanted to correct some mistakes or flaws in a paper that he or she just published, but there's never been a good mechanism for that. Furthermore, the current model of peer review normally involves only two or three referees for each submission, and this limited number of minds and eyes can easily produce biased or careless comments. Post-publication peer review helps to provide a better, less-biased assessment of the research.

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Attachment bonds between domestic cats and humans

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Worldwide, domestic cats (*Felis silvestris catus*) outnumber domestic dogs (*Canis familiaris*). Despite cats' success in human environments, dog social cognition has received considerably more scientific attention over the last several decades [1–3]. A key aspect of what has been said to make dogs unique is their proclivity for forming attachment bonds, including secure attachments to humans [1,3], which could provide scaffolding for the development of human-like socio-cognitive abilities and contribute to success in human environments [3]. Cats, like dogs, can be found living in social groups or solitarily, depending on early developmental factors, resource distribution, and lifetime experiences such as human interaction [1,2,4]. Despite fewer studies, research suggests we may be underestimating cats' socio-cognitive abilities [2]. Here we report evidence, using behavioral criteria established in the human infant literature [5,6], that cats display distinct attachment styles toward human caregivers. Evidence that cats share social traits once attributed to dogs and humans alone would suggest that broader non-canine-specific mechanisms may be needed to explain cross-species attachment and socio-cognitive abilities.

In our study, cats and owners participated in a Secure Base Test (SBT), an abbreviated strange situation test used to evaluate attachment security in primates [7] and dogs [8]. During this test, the subject spends 2 minutes in a novel room with their caregiver, followed by a 2-minute alone phase, and then a 2-minute reunion phase (see Supplemental Information for details). Cats were classified into attachment styles by expert attachment coders using the same criteria used in the human infant [5,6] and dog literature [8,9]. Upon the caregiver's return from a brief absence, individuals with secure attachment display a reduced stress response and contact-exploration balance with the

caretaker (the Secure Base Effect), whereas individuals with an insecure attachment remain stressed and engage in behaviors such as excessive proximity-seeking (ambivalent attachment), avoidance behavior (avoidant attachment), or approach/avoidance conflict (disorganized attachment) [6].

The SBT was conducted with kittens aged 3–8 months. Seventy kittens were classified into an attachment style (see Supplemental Information) and 9 kittens were unclassifiable. Of the classifiable kittens, 64.3% were categorized as securely attached and 35.7% were categorized as insecurely attached (Figure 1). Of the insecure kittens, 84% were ambivalent, 12% avoidant, and 4% disorganized. To determine if attachment style could be predicted by differential socialization and reinforcement opportunities alone, a portion of the kittens were enrolled in a 6-week training and socialization intervention with their caretaker following baseline. When comparing 39 class and 31 control kittens, there were no significant differences in the number of kittens classified as secure or insecure either at baseline (Fishers, $p = 0.14$) or approximately 2 months later at follow-up (Fisher's, $p = 1.0$). These results indicate that although social reinforcement is likely a factor that contributes to the development of an attachment style, once an attachment style has been established between the members of a dyad, it appears to remain relatively stable over time, even after a training and socialization intervention [5]. Indeed, we found the proportion of secure and insecure kittens at follow-up mirrored that of baseline, with 68.6% displaying secure attachment and 31.4% displaying insecure attachment. At the individual level, 81% of kittens retained the same secure base designation (secure/insecure) at retest (Binomial, $p < 0.0001$). This may suggest that heritable factors, such as temperament, also influence attachment style and could contribute to its stability.

Because cats, like most domesticated animals, retain several juvenile traits into maturity and remain dependent on humans for care, we predicted that attachment behavior toward a primary caretaker would be present in adulthood. To evaluate this, 38 cats over one year of age participated in the SBT. Distinct attachment styles were evident in



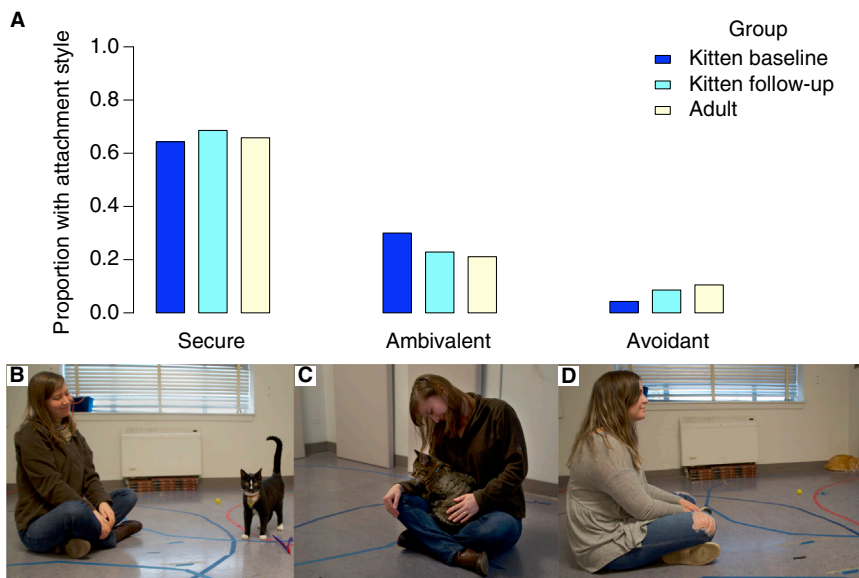


Figure 1. The main attachment styles observed in the cat-human bond.

(A) Proportion of three main attachment styles observed in kittens and adult cats. (B) Cat with secure attachment. (C) Cat with insecure-ambivalent attachment. (D) Cat with insecure-avoidant attachment.

adult cats (Figure 1), with a distribution similar to the kitten population (65.8% secure, 34.2% insecure). To evaluate the possibility that differences between cats classified as secure or insecure could be attributed to different responses to stressful situations rather than distinct responses to the return of the owner, we evaluated the frequency of meow vocalizations produced in the alone phase of the SBT as a measure of separation distress. Attachment theory predicts that both secure and insecure-ambivalent individuals should show signs of distress including vocalizations during this phase with little difference between secure and insecure-ambivalent individuals [5]. Insecure-avoidant and disorganized individuals should show less separation distress [5]. As predicted, cats categorized as secure or insecure-ambivalent showed equivalent levels of separation distress in the alone phase as measured by vocalization frequency ($U(32) = 68.5$, $Z = -0.843$, $p = 0.40$; see Video S1 Timestamp 8:08), and both groups showed significantly more attachment distress than insecure-avoidant and disorganized cats ($H(2) = 7.39$, $p = 0.025$).

Overall, indicators of attachment relationships between cats and humans, including proximity seeking, separation distress and reunion behavior, were present, and individual differences

in response were consistent with attachment style categorizations as previously described in the literature. The current data support the hypothesis that cats show a similar capacity for the formation of secure and insecure attachments towards human caregivers previously demonstrated in children (65% secure, 35% insecure) [10] and dogs (58% secure, 42% insecure) [8,9] with the majority of individuals in these populations securely attached to their caregiver. Cat attachment style appears to be relatively stable and is present in adulthood. In free-roaming settings both cats and dogs are facultatively social species and live individually or in groups based on environmental pressures and availability of resources [1,2,4]. Our study provides evidence that this social flexibility extends to cross-species attachments, suggesting that, like dogs, cats are social generalists [1]. Attachment to humans may represent a flexible adaptation of offspring-caregiver attachment that has facilitated success in anthropogenic environments.

SUPPLEMENTAL INFORMATION

Supplemental information includes supplemental experimental procedures, supplemental references, and one video and can be found with this article online at <https://doi.org/10.1016/j.cub.2019.08.036>.

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AUTHOR CONTRIBUTIONS

Conceptualization, K.V. and M.U.; Methodology, K.V. and M.U.; Analysis, K.V. and M.U.; Investigation, K.V. and A.B.; Writing – Original Draft, K.V. and M.U.; Writing – Review & Editing, K.V., M.U., and A.B. Visualization, K.V., Supervision K.V. and M.U.; Funding Acquisition K.V. and M.U.

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