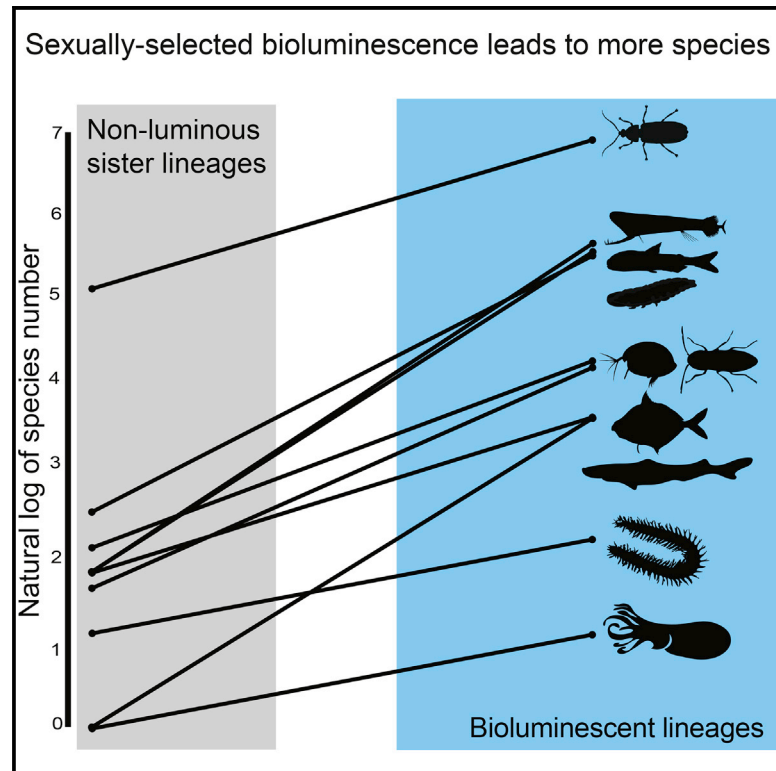


# Current Biology

## High Rates of Species Accumulation in Animals with Bioluminescent Courtship Displays

### Graphical Abstract



### Authors

Emily A. Ellis, Todd H. Oakley

### Correspondence

oakley@lifesci.ucsb.edu

### In Brief

Ellis and Oakley find compelling evidence for sexual selection contributing to bursts in species accumulation across a wide diversity of animal lineages. They show that animals with bioluminescent courtship have more species than their non-luminous sister clades, a pattern not found in animals with bioluminescent camouflage.

### Highlights

- Lineages with bioluminescent courtship are associated with high species richness
- Bioluminescent camouflage has no association with species richness
- Sexually selected traits may drive macroevolutionary increases in speciation rate



# High Rates of Species Accumulation in Animals with Bioluminescent Courtship Displays

Emily A. Ellis<sup>1</sup> and Todd H. Oakley<sup>1,\*</sup>

<sup>1</sup>Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, Santa Barbara, CA 93106, USA

\*Correspondence: [oakley@lifesci.ucsb.edu](mailto:oakley@lifesci.ucsb.edu)

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## SUMMARY

One of the great mysteries of evolutionary biology is why closely related lineages accumulate species at different rates. Theory predicts that populations undergoing strong sexual selection will more quickly differentiate because of increased potential for genetic isolation [1–6]. Whether or not these population genetic processes translate to more species at macroevolutionary scales remains contentious [7]. Here we show that lineages with bioluminescent courtship, almost certainly a sexually selected trait, have more species and faster rates of species accumulation than their non-luminous relatives. In each of ten distantly related animal lineages from insects, crustaceans, annelid worms, and fishes, we find more species in lineages with bioluminescent courtship compared to their sister groups. Furthermore, we find under a Yule model that lineages with bioluminescent courtship displays have significantly higher rates of species accumulation compared to a larger clade that includes them plus non-luminous relatives. In contrast, we do not find more species or higher rates in lineages that use bioluminescence for defense, a function presumably not under sexual selection. These results document an association between the origin of bioluminescent courtship and increased accumulation of species, supporting theory predicting sexual selection increases rates of speciation at macroevolutionary scales to influence global patterns of biodiversity.

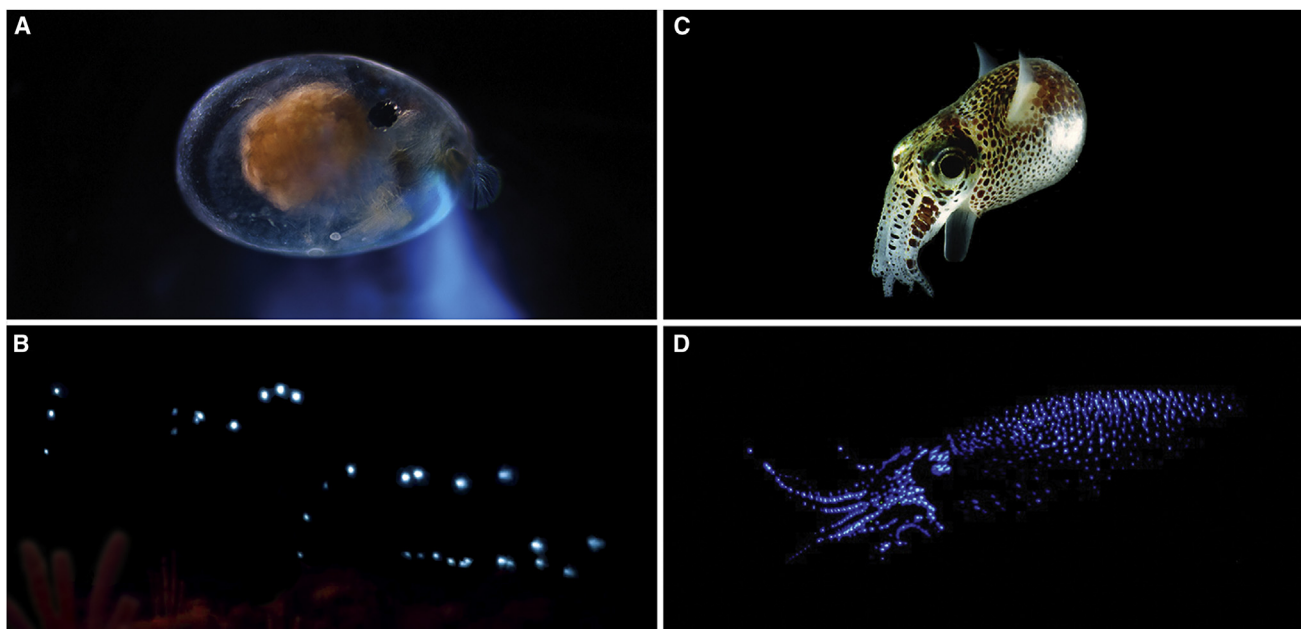
## RESULTS AND DISCUSSION

Why some traits seem to be associated with rapid formation of species (speciation) and others are associated with rapid loss of species (extinction) has long perplexed naturalists. Identifying these traits and linking evolutionary mechanisms to shifts in species accumulation is a central goal in the study of global biodiversity and evolutionary biology. Traits strongly influenced by sexual selection might influence species accumulation (diversification) (e.g., [1–6]). If male trait and female preference co-evolve [6] and there is sufficient genetic variation in both [5], isolated populations will diversify with respect to sexually selected traits [6]. The evolutionary processes driving the initial differences in sexu-

ally selected traits include intra-specific competition [2], genetic instability [4], genetic drift [5], environmental effects [8], and avoidance of predators [1, 9]. Each of these mechanisms may result in assortative mating within populations and lead to effective reproductive isolation and new species. This strong population genetic foundation [10] suggests that sexual selection not only should contribute to phenotypic diversification, but also may affect rates of species accumulation at macroevolutionary scales. Although empirical studies show a clear link between sexual selection and phenotypic diversification (e.g., [11–13]), whether or not sexual selection generally influences rates of species accumulation on macroevolutionary scales is still a matter of debate [14, 15] because empirical support remains ambiguous.

Overall, review of the literature on comparative studies of the relationship between sexual selection and rates of species accumulation identifies at least three obstacles to strong, general conclusions from empirical data. First, most studies use indirect proxies for the strength of sexual selection, including genital size, mating system, size dimorphism, and degree of dichromatism. Unfortunately, the correlation between these proxies and the actual strength of sexual selection is difficult to determine and is not comparable across animal groups [7]. Second, studies often do not exclusively include independent origins of the sexual trait in question, but instead combine origins and losses. This is important because evolutionary processes in lineages in which the trait is gained versus lost are most likely different. Third, most studies focus on a single taxonomic group at a time—most commonly birds [7]. For example, Barraclough et al. [16] first found a strong correlation between a proxy of sexual selection and species diversity in birds. Although many subsequent studies in birds and some other taxa find similar positive relationships (e.g., [17–19]), many others find none at all (e.g., [20, 21]), sometimes even when using similar datasets [22]. Although meaningful in their own right, it is impossible to make taxonomically widespread conclusions from these studies on single groups. An improved study would use an easily interpretable, sexually selected trait, include only independent origins of the trait in question, and encompass a wide taxonomic breadth.

For these reasons, bioluminescence is an excellent trait to test whether a sexually selected trait leads to more species. First, like other courtship displays, bioluminescent mating signals are almost certainly influenced by sexual selection. Luminous courtship displays (Figure 1) are information rich and sexually dimorphic, allowing for direct female choice [23]. Consistent with sexual selection, the operational sex ratio of species using luminous courtship displays is usually drastically skewed toward the signaling sex [23]. Luminous courtship signals may also evolve to maximize sensory stimulation, which often leads to



**Figure 1. Composite Image Showing Examples of Bioluminescent Courtship and Counterillumination Displays and Animals that Produce Them**

(A) Bioluminescent ostracods of the family Cypridinidae (image courtesy Elliot Lowndes: [elliott@mrLOWndes.com](mailto:elliott@mrLOWndes.com), [www.mrLOWndes.com](http://www.mrLOWndes.com)).

(B) An ostracod displaying bioluminescent courtship (image created in Photoshop by T.H.O.).

(C) An example of a squid that exhibits counter-illumination (image courtesy National Science Foundation).

(D) A squid displaying bioluminescent counter-illumination (image courtesy Danté Fenolio).

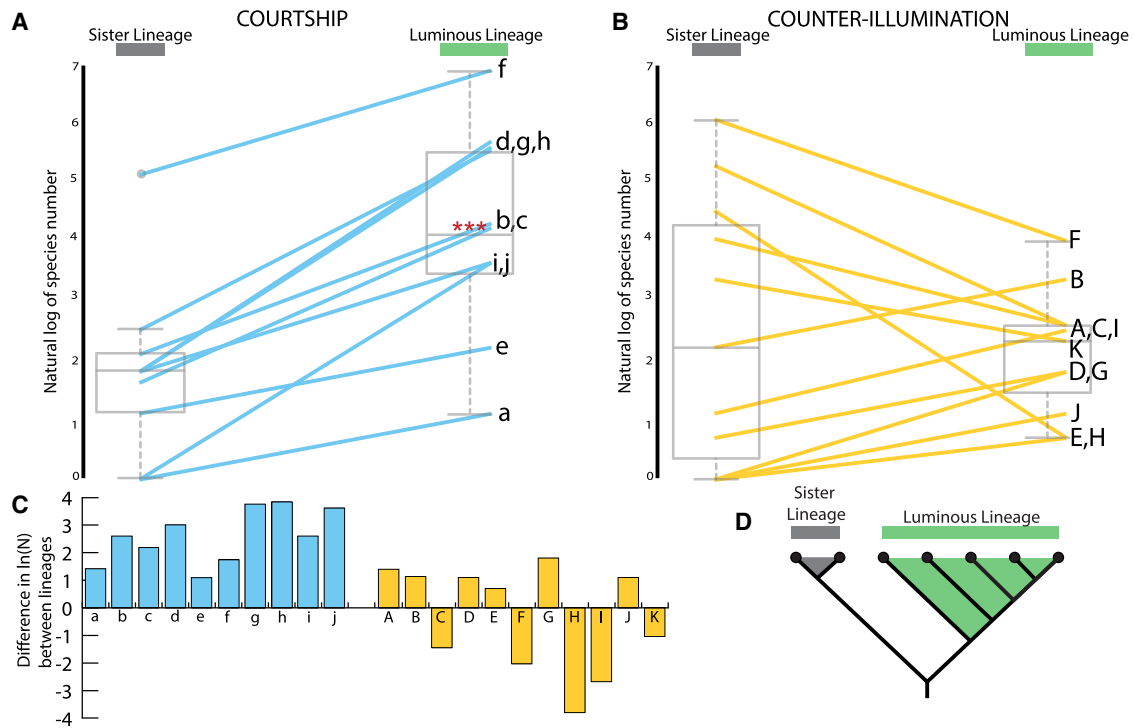
progressively more conspicuous signals via elaboration over evolutionary time [24]. In addition to its use in sexually selected courtship, bioluminescence is used for other adaptive functions, including defense (e.g., camouflage by counter-illumination; Figure 1) and predation [25]. In several cases, the biochemistry, genetic basis, and phylogenetic history of light production are understood, allowing for strong inferences about gain and loss of the trait. In all, light production evolved separately at least 40 times in a wide diversity of marine and terrestrial animals [25]. Therefore, the numerous origins of light production allow for comparisons of species accumulation in taxa with vastly different ecological roles. Our comparisons indicate that bioluminescent lineages have more species and often significantly higher rates of species accumulation when they use light for courtship displays, but not when they use light for camouflage. We argue bioluminescent courtship displays provide unusually clear empirical support for the strong theoretical prediction that sexually selected traits are an engine of speciation.

We compiled phylogenetic and taxonomic literature, including estimates of divergence times, for bioluminescent lineages and their close relatives (Tables S1–S3). We used these data for two main analyses. In each analysis, we separated lineages that use light for courtship (probably under sexual selection) from lineages that use light for counter-illumination camouflage (presumably not under sexual selection). Our first analysis (Figure 2; Table S1) compared the number of species of each bioluminescent lineage to the number of species in its closest non-luminous sister lineage. Our second analysis (Figure 3; Table S2) assumed a pure-birth process of cladogenesis and asked whether each individual bioluminescent lineage showed

a higher rate of species accumulation compared to its greater taxonomic group (we call the larger groups the “encompassing clades,” which each include the focal bioluminescent clade, non-luminous sister clade, and other non-luminous relatives; see Figure 3D).

We find that lineages using light for courtship, a sexually selected trait, have significantly more species than their sister lineages. Compared to their closest non-luminous sister groups, lineages that possess bioluminescent courtship displays have more species in each of ten independent comparisons, across a diverse set of animals (Figure 2). On average, the ten lineages that use light for courtship have more species than the average of their closest sister lineages (Figure 2; two-tailed  $p = 0.0001$ ; Table S4). In contrast, lineages that use light for counter-illumination camouflage, on average, do not differ in species number from their non-luminous sister lineages (Figure 2; two-tailed  $p = 0.5693$ ; Table S4).

We next found that the differences in species number between sister lineages are not caused by a decreased rate of species accumulation in non-luminous lineages but, rather, by faster accumulation of species in lineages with bioluminescent courtship. Specifically, we asked whether each separate origin of luminous courtship showed an increase in estimated rate of species accumulation compared to the rate of a larger encompassing clade (see Figure 3D). Out of ten cases, seven had divergence time estimates available for this test (see the Supplemental Experimental Procedures, Section S1). Of those seven, we found four lineages with significant increases in rates of species accumulation when compared to the rate of their greater taxonomic group (cypridinid ostracods, myctophid



**Figure 2. Lineages with Bioluminescent Courtship Have More Species Than Their Non-luminous Sister Lineages**

(A and B) Slope lines link the natural log of species number for non-luminous taxa (left) with their luminous sister lineage (right) for taxa that exhibit bioluminescent courtship (A, blue) and bioluminescent counter-illumination (B, yellow). Box plots depict data distributions. Lineages are labeled as follows: a, bolitaenin octopus; b, cyprinid ostracod; c, pyrophorin click beetle; d, rhagophthalmid railroad beetle; e, syllid polychaete; f, lampyrin and photurin firefly; g, myctophid lanternfish; h, stomiid dragonfish; i, gazzin ponyfish; j, *Etmopterus* shark; A, loliginid squid; B, sepiolid squid; C, oplophorid shrimp; D, *Neoscoelus* blackchin; E, *Coccorella* sabertooth fish; F, alepocephaloid slickhead; G, *Rhabdamia* cardinalfish; H, *Archamia* cardinalfish; I, leiognathin ponyfish; J, lestitiid naked barracudina; K, dalatiid shark.

(C) The bar graph shows the difference in species number (in natural log) between luminous lineages and their non-luminous sister lineages.

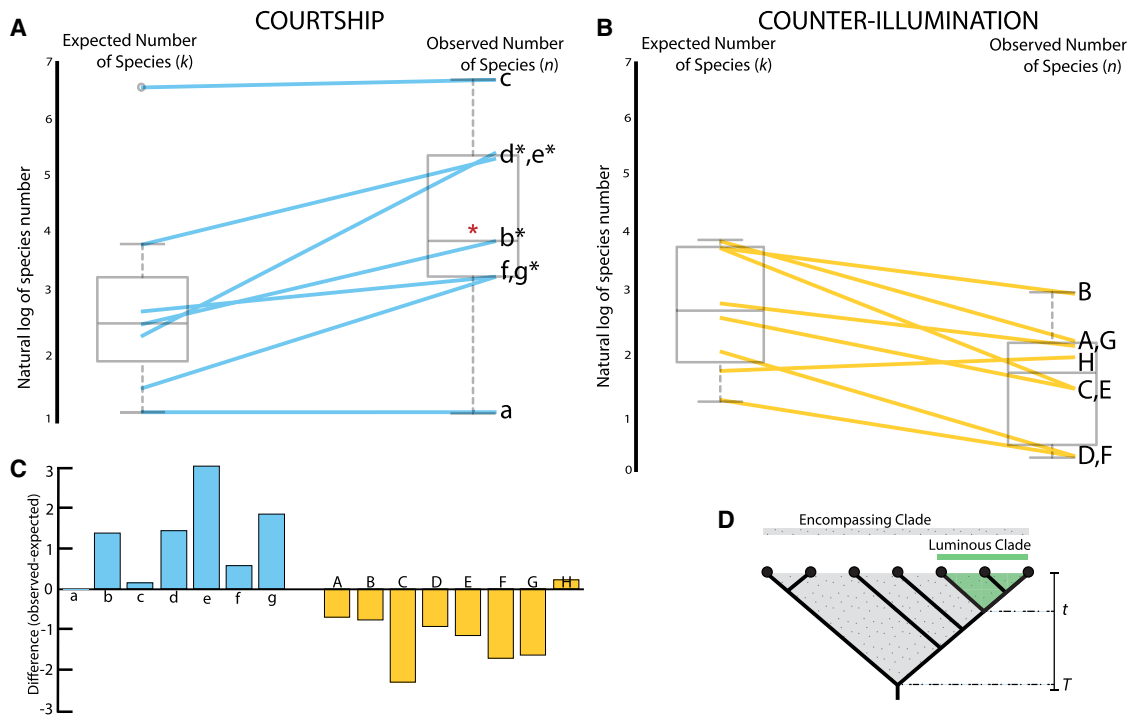
(D) The distinction between the luminescent lineage and the non-luminescent sister lineage, the source of all comparisons in this figure.

See also Tables S1, S3, and S4.

lanternfishes, stomiid dragonfishes, and *Etmopterus* lantern sharks; Figure 3; Table S2). When averaging across all seven of these clades, we found that lineages with luminescent courtship possess significantly more species than expected from the rate of species accumulation estimated from their older, encompassing clade (two-tailed  $p = 0.0251$ ). In contrast, a single lineage of bioluminescent counter-illuminating species (of eight), dalatiid lantern sharks, display a non-significant increase in rate when compared to their greater taxonomic group. In other words, a decrease in rate of species accumulation in non-luminous lineages does not explain why luminous courting lineages have more species. In fact, counter-illuminating lineages on average possess significantly fewer species than expected (two-tailed  $p = 0.0086$ ), consistent with diversity-dependent species accumulation, a prevailing pattern in recent macroevolutionary studies [26, 27].

The magnitude of our results is surprising because the diminishing rate of species accumulation through time due to diversity dependence would make our second test (Figure 3) very conservative. Our calculations predict species number in younger, luminous lineages based on rates calculated from older, encompassing clades (Figure 3; Table S2). Under diversity dependence, younger lineages have slower rates of species accumulation,

which would result in systematic overestimates of predicted species number using constant rates. In fact, diversity dependence may explain the pattern that we find in counter-illuminating lineages: significantly fewer species are observed than predicted from rates of an older lineage (Figure 3). Despite this conservatism (which is perhaps even a strong bias against finding a significant result), we still find significantly more species than expected in courting lineages. We further tested a prediction of diversity dependence by instead calculating expected species number of each older, encompassing clade using the species accumulation rate of each younger, bioluminescent clade (Table S2). If diversity dependence has influenced species accumulation, we expect that each luminous lineage's accumulation rate would underestimate species number of their older encompassing clades. Whereas counter-illuminating lineages fit this pattern of diversity dependence (one-tailed  $p = 0.00275$ ), courting lineages show the opposite: they significantly overestimate encompassing clade species number (one-tailed  $p = 0.0366$ ). Therefore, courting lineages display an exceptionally high rate of species accumulation, especially if species accumulated in a diversity-dependent manner. Thus, the origin of bioluminescent courtship, most likely under sexual selection, is associated with a significant increase in species accumulation rates.



**Figure 3. Six Lineages with Bioluminescent Courtship Have More Species Than Predicted from Estimates of Average Background Species Accumulation Rate**

(A and B) Slope lines link the natural log of expected (left) and observed (right) species number for eight bioluminescent courtship (A, blue) and counter-illuminating (B, yellow) lineages. We calculated expected species number using the average species accumulation rate of the encompassing clade (see D). Lineage labels are as follows: a, bolitaenid octopus; b, cypridinid ostracod; c, lampyrid and photurid firefly; d, myctophid lanternfish; e, stomiid dragonfish; f, gazzin ponyfish; g, *Etmopterus* shark; A, loliginid squid; B, sepiolid squid; C, *Neoscopelus* lanternfish; D, *Coccorella* sabertooth fish; E, *Rhabdamia* cardinalfish; F, *Archamia* cardinalfish; G, leiognathin ponyfish; H, dalatiid shark. Black asterisks indicate lineages in which the observed species number in the bioluminescent lineage is significantly greater than the expected species number (Table S2).

(C) The bar graph shows the difference between observed and expected species number (in natural log).

(D) The encompassing clade (lineage), which is defined as the higher taxonomic group that includes the bioluminescent clade (lineage). We calculated average species accumulation rate using the clade age and extant species number of the encompassing clade. We then solved for expected species number of the bioluminescent clade using the age of the bioluminescent clade and the species accumulation rate of the encompassing clade.

See also Table S2 and Data S1.

Given the conflicting history of studies exploring a potential association between sexual selection and speciation, the clarity and consistency of our results may appear surprising. Therefore, it is important to consider caveats and assumptions for the strong pattern. First, luminous courting lineages may be more conspicuous and suffer from discovery bias. Although we are unable to completely discount this alternative, we note that even if published phylogenies do not contain all species, many of the groups (luminous and nonluminous species) included in our analysis are taxonomically well studied (e.g., fishes and fireflies), allowing less potential for description bias. Of those that are not well studied, many are deep-sea and pelagic species caught non-visually with dredges and plankton nets, such that luminous species would not be more conspicuous to taxonomists. Second, we rely on the accuracy of phylogenetic hypotheses for our results. We only analyzed well-sampled lineages with well-supported placement of bioluminescent lineages (Table S1). Importantly for both of these assumptions, our analyses include a natural control of a bioluminescent trait that most likely does not evolve by sexual selection. If taxonomists have a strong bias for bioluminescent species, or if phylogenetic

uncertainty caused systematic bias, we might expect to find a pattern of increased species number in all bioluminescent lineages, not only those using light for courtship.

Our results show that lineages with bioluminescent courtship displays under sexual selection always accumulated more species than their close relatives without the trait, often after a significant increase in rate of species accumulation compared to their larger taxonomic group. Despite our inability with current data and analytical methods [28] to disentangle speciation and extinction rates, we suggest that our results are driven by increases in speciation rate, as opposed to decreases in extinction rate. First, sexual selection over macroevolutionary time probably increases extinction rate. Even though a recent study used artificial selection to show increased persistence of laboratory populations under strong sexual selection in the absence of predators [29], other studies that investigated this question in a natural, macroevolutionary context showed the opposite—more extinction in lineages with strong sexual selection [30, 31]. If sexual selection causes more extinction on macroevolutionary timescales, then our result of more species would require even faster rates of speciation to offset increased extinction.

Long predicted by population genetic theory, our results are consistent with sexual selection as an important driver of macroevolutionary patterns of species accumulation, probably through increased rates of speciation after the origin and maintenance of a sexually selected trait. Therefore, sexual selection may have a strong impact on global biodiversity.

## EXPERIMENTAL PROCEDURES

### Literature Search

We used taxonomic reviews [25, 32–36] to identify bioluminescent lineages. We then determined whether bioluminescence functions as a courtship display (if studies support its use in mating; Table S1) or used for counter-illumination (defined as possessing ventral photophores; Table S1). We next compiled published phylogenies that include exemplars of luminous and close relatives to determine the non-luminous sister lineage to each luminous lineage (Table S1). We were unable to analyze the data using methods such as BiSSE (binary state speciation and extinction) [37] because of possible concerns with overparameterization [38] and because phylogenies with less than 20% taxon sampling were common in our dataset, which would lead to uncertain parameter estimates [39]. We required good support (>70% bootstrap support) for monophyly of the focal lineage and an exemplar of every taxon of equal rank to the luminous lineage to be included in the phylogeny to ensure adequate taxon sampling to determine sister-group status (see the Supplemental Experimental Procedures, Section S1). We obtained species number of lineages from original species descriptions, and cross-referenced with the World Register of Marine Species (WoRMS), Encyclopedia of Life, and FishBase databases [40–42]. We did not include species that secondarily lost the bioluminescent function in the total species counts for the luminous lineages. In total, we identified 17 lineages with bioluminescent courtship (Tables S1 and S3). Of those, ten have sufficiently well-supported lineage splits, adequate taxon sampling, and sufficient evidence to support a courtship function of bioluminescence to use in our analyses (Table S1). Similarly, we identified 23 lineages with bioluminescent counter-illumination (Table S3), with 11 having adequate phylogenetic information to allow further analysis (Table S1).

### Sister Lineage Analysis

We followed Rabosky [43] to calculate rates of species accumulation in lineages of equal age (sister clades), where  $\Omega$  is the natural log of species number (number of species). We used a one-sample *t* test to determine the significance of differences in average numbers of species between sister lineages. We calculated  $\Delta\Omega$  by subtracting  $\Omega$  (nonluminous) from  $\Omega$  (luminous). We then compared  $\Delta\Omega$  to a hypothetical mean of zero in a one-sample *t* test. We also performed randomization tests for matched pairs ( $N = 10$ ) and Wilcoxon signed-rank tests ( $N \geq 10$ ) using the python program SYSTEMS [44] to determine the probability that the distribution of species accumulation rate between luminous and non-luminous lineages might best be explained by chance (Table S4).

### Testing for Increases in Rate of Species Accumulation

We tested for a significant increase in rate of accumulation of species in each focal (luminous) lineage compared to the accumulation rate of species in an encompassing clade, which we define as a larger group of species including luminous and non-luminous species (Figure 3D). More specifically, we defined each encompassing clade to be one taxonomic rank more inclusive than each luminous clade. For example, if luminous genera comprise the focal lineage, then the entire family is the encompassing clade.

We used equations for a pure-birth model of cladogenesis to determine the expected number of species in each bioluminescent lineage, assuming that they shared the same rate of species accumulation as their encompassing clade. First, using Geiger [45], we estimated this rate ( $R$ ) in each encompassing clade using

$$(\log(N) - \log(2))/T,$$

where  $N$  is the number of species in each encompassing clade and  $T$  is the time of origin of each encompassing clade, taken from phylogenetic studies

that employed relaxed molecular clock methods (Table S2; or calculated in this study—see the Supplemental Experimental Procedures, Section S2).

Assuming  $R$ , we then calculated the expected number of species ( $k$ ) in each luminous lineage based on its age ( $t$ ). If luminous clade have faster rates of species accumulation than their encompassing clade, observed species number ( $n$ ) in the luminous clade will be higher than  $k$ . To calculate  $k$ , we followed Magallón and Sanderson [46], equation 11:

$$P[N(t) \geq k] = \beta^k (k - 2) [k(1 - \beta) + 2\beta - 1],$$

where shape parameter

$$\beta = (e^{\wedge}(Rt) - 1) / e^{\wedge}(Rt).$$

We numerically solved for  $k$ , which depends on  $R$  and  $t$ , the mean clade age of the focal (luminous) clade (obtained from the same study as the encompassing clade age; Table S2). To obtain the upper bound on the 95% confidence interval, we solved for  $k$  where  $P[N(t) \geq k] = 0.025$ , the point in the distribution below which 97.5% of the replicates of the stochastic process will lie. Likewise, we solved for  $k$  where  $P[N(t) \geq k] = 0.0975$  to determine the point above which 97.5% of the replicates will lie. We then solved for  $k$  where  $P[N(t) \geq k] = 0.50$  to determine the mean of expected species number. If the observed species number of the bioluminescent clade was outside of the 95% confidence interval, we deemed it statistically significant (marked by an asterisk in Figure 3). Lastly, we converted raw species number to  $\Omega$  by taking the natural log of raw species number [43]. To test whether a model of diversity-dependent species accumulation would change our results, we used similar calculations, but in reverse. Instead of determining the number of species expected in each bioluminescent clade, we determined (still using a constant-rate model) the expected number of species in each encompassing clade, assuming that they share the same rate of species accumulation as the younger, bioluminescent clade. If diversity dependence holds, the size of an older lineage (like the encompassing clade) would be larger than expected from rates of the younger lineage. A more formal test of diversity dependence is not possible because it requires estimates of carrying capacity and the magnitude of rate change, which are unavailable without nearly complete phylogenies at the species level.

## SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, four tables, and one data file and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.05.043>.

## AUTHOR CONTRIBUTIONS

Conceptualization, E.A.E. and T.H.O.; Methodology, E.A.E. and T.H.O.; Investigation, E.A.E. and T.H.O.; Visualization, E.A.E. and T.H.O.; Writing, E.A.E. and T.H.O.; Funding Acquisition, T.H.O.

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