



Resembling a Viper: Implications of Mimicry for Conservation of the Endangered Smooth Snake

JANNE K. VALKONEN* AND JOHANNA MAPPE

Department of Biological and Environmental Science, Centre of Excellence in Biological Interactions, University of Jyväskylä, P.O. Box 35, Jyväskylä 40014 Finland

Abstract: *The phenomenon of Batesian mimicry, where a palatable animal gains protection against predation by resembling an unpalatable model, has been a core interest of evolutionary biologists for 150 years. An extensive range of studies has focused on revealing mechanistic aspects of mimicry (shared education and generalization of predators) and the evolutionary dynamics of mimicry systems (co-operation vs. conflict) and revealed that protective mimicry is widespread and is important for individual fitness. However, according to our knowledge, there are no case studies where mimicry theories have been applied to conservation of mimetic species. Theoretically, mimicry affects, for example, frequency dependency of predator avoidance learning and human induced mortality. We examined the case of the protected, endangered, nonvenomous smooth snake (*Coronella austriaca*) that mimics the nonprotected venomous adder (*Vipera berus*), both of which occur in the Åland archipelago, Finland. To quantify the added predation risk on smooth snakes caused by the rarity of vipers, we calculated risk estimates from experimental data. Resemblance of vipers enhances survival of smooth snakes against bird predation because many predators avoid touching venomous vipers. Mimetic resemblance is however disadvantageous against human predators, who kill venomous vipers and accidentally kill endangered, protected smooth snakes. We found that the effective population size of the adders in Åland is very low relative to its smooth snake mimic (28.93 and 41.35, respectively). Because Batesian mimicry is advantageous for the mimic only if model species exist in sufficiently high numbers, it is likely that the conservation program for smooth snakes will fail if adders continue to be destroyed. Understanding the population consequences of mimetic species may be crucial to the success of endangered species conservation. We suggest that when a Batesian mimic requires protection, conservation planners should not ignore the model species (or co-mimic in Mullerian mimicry rings) even if it is not itself endangered.*

Keywords: conservation, *Coronella austriaca*, mimicry, predation, snake, viper, *Vipera berus*, warning signal

Implications of mimicry for Conservation of the endangered smooth snake

Resumen: *El fenómeno del mimetismo batesiano, en el cual un animal apetitoso adquiere protección contra la depredación al asemejarse a un modelo no apetitoso, ha sido un interés nuclear de los biólogos evolucionistas durante 150 años. Una gama extensa de estudios se ha enfocado en revelar los aspectos mecánicos del mimetismo (educación compartida y generalización de los depredadores) y las dinámicas evolutivas de los sistemas de mimetismo (cooperación vs conflicto), y esta reveló que el mimetismo protector está ampliamente distribuido y es importante para la aptitud individual. Sin embargo, de acuerdo con nuestro conocimiento, no existen estudios de caso donde las teorías de mimetismo se han aplicado a la conservación de especies miméticas. En teoría, el mimetismo afecta por ejemplo, la frecuencia de dependencia del aprendizaje de evasión de depredadores, y evita la mortalidad inducida por humanos. Examinamos el caso de la serpiente lisa no venenosa *Coronella austriaca* que se encuentra protegida y en peligro de extinción, y que mimetiza a la víbora venenosa *Vipera berus*, que no se encuentra protegida. Ambas especies habitan en el archipiélago Åland, en Finlandia. Para cuantificar el riesgo de depredación añadido a las serpientes lisas causado por la*

*email janne.k.valkonen@ju.fi

Paper submitted December 20, 2013; revised manuscript accepted May 8, 2014.

rareza de las víboras, calculamos estimados de riesgo a partir de datos experimentales. La semejanza entre las serpientes y las víboras mejora la supervivencia de las serpientes lisas a la depredación de aves ya que muchos depredadores evitan entrar en contacto con víboras venenosas. Sin embargo, la semejanza mimética es una desventaja contra los depredadores humanos, ya que matan a las víboras venenosas y accidentalmente matan a las serpientes lisas, en peligro de extinción y protegidas. Encontramos que el tamaño poblacional efectivo de las víboras en Åland es muy bajo en relación a su imitador, la serpiente lisa (28.93 y 41.35, respectivamente). Ya que el mimetismo batesiano es una ventaja para el imitador sólo si la especie modelo existe en números suficientemente altos, es probable que el programa de conservación para la serpiente lisa falle si se sigue cazando a las víboras. Entender las consecuencias poblacionales de las especies miméticas puede ser crucial para el éxito de la conservación de la especie en peligro. Sugerimos que cuando un imitador batesiano requiera protección, quienes planeen la conservación no ignoren a la especie modelo (o imitador simultáneo en los anillos de mimetismo mullerianos), aunque esta no se encuentre en peligro.

Palabras Clave: conservación, *Coronella austriaca*, depredación, mimetismo, señal de advertencia, serpiente, víbora, *Vipera berus*

Introduction

Many prey species are chemically defended, venomous, or toxic, and some of them advertise their unprofitability to potential predators with warning colors, odors, behavior, or sounds (Ruxton et al. 2004). Predators learn to associate the unpleasant experience of an encounter with the warning signal and then avoid similar encounters in future encounters. Many profitable species in turn have evolved to mimic warning signals of defended species to avoid attacks by predators. Thus, prey animals can use predators' tendencies to generalize their learned avoidance to similar signals as protective mimicry (Bates 1862; Müller 1879; Poulton 1890).

In Batesian mimicry, palatable species mimic the appearance of an unpalatable model and gain protection from predation because predators misclassify them as a defended model species (Bates 1862). Models should thus be relatively common, and usually more common than mimics, because otherwise predators' avoidance learning would degrade (Cott 1940; Lindström et al. 1997). The importance of abundance of the model in the Batesian mimicry system is intuitively easy to understand because predators' avoidance learning and memory are based on unpleasant encounters with the model (Huheey 1964). However, determining what abundance of the model is sufficient to protect Batesian mimics is not so simple because it can depend on several factors, including accuracy of the mimicry and potency of the defense of the model (Lindström et al. 1997; Mappes & Alatalo 1997; Harper & Pfennig 2007). Nevertheless, if the number of models decreases, the benefits gained by a mimic also decrease. Furthermore, if the relative abundance of the mimic increases excessively relative to the model, then the benefits of the warning signal to the model can also be diluted because predators' avoidance learning and memory may be undermined through experience with the mimic (Huheey 1964). It is also important to remember that mimic and model (or co-mimics) do not need to be

strictly sympatric (Pfennig & Mullen 2010), they just need to share predator population.

Protective mimicry is widespread across the animal kingdom and can take many forms. A lacertid lizard mimics a noxious beetle by its coloration and walking behavior (Huey & Pianka 1977) and butterfly species in Amazonian Ecuador form several mimicry rings (i.e., groups of species that have similar warning coloration) that include multiple noxious and palatable species (Bates 1862; Beccaloni 1997a, 1997b). Mimics can be expected to be under strong selection toward accurate resemblance of the model because of enhanced avoidance learning (Mappes & Alatalo 1997; Symula et al. 2001). The accuracy of mimicry also enhances the probability that predators will misclassify the mimic as an unpalatable model and refrain from attacking it (Caley & Schluter 2003). Because a predator's decision to attack mimics can be based on the risk of accidentally attacking a noxious model, it is possible that accurate mimics can benefit from protection against predation even if the model is relatively rare, especially if it is deadly (Harper & Pfennig 2007). However, in the case of human predation, one can expect both abundance of the model and accuracy of mimicry to increase mortality of the mimic because there is no cost of attacking the model. If the model is not avoided and is persecuted by humans, accurate mimicry can turn out to be extremely costly for the mimics. Similarly, if a foreign predator that does not avoid local defended models (and thereby mimic species) invades the area, the benefits of this evolved antipredator strategy can vanish possibly with dramatic consequences.

Mimicry seems to be common among snakes, including the famous example of a mimicry ring of venomous coral snakes and their mimics (reviewed in Brodie & Brodie 2004). The risk of getting injured during the attack of a defended model affects predator avoidance and makes mimicking a highly toxic or dangerous model beneficial, which can explain why venomous snakes are often mimicked (Brodie & Brodie 2004). Mimicking venomous

snakes can be highly advantageous for nonvenomous species because of the strong avoidance of predators (e.g., Pfennig et al. 2001). For example cephalopods are known to mimic venomous sea snakes by changing their color and adopting a snake-like posture when they retreat to a burrow and expose two arms extended in opposite directions (Norman et al. 2001). Several butterfly larvae mimic snakes by inflating their thorax or abdomen and exposing false eyes (e.g., Bates 1862; Berenbaum 1995; Hossie & Sherratt 2014). Many nonvenomous snakes gain protection against predation by resembling venomous snakes in their appearance (reviewed in Brodie & Brodie 2004).

Snake populations are declining at a substantial rate across the globe (Reading et al. 2010). Therefore, the number of species in need of conservation is increasing, and vast attention is being paid to the causes and consequences of habitat loss and fragmentation and to genetic structuring of populations (e.g. Filippi & Luisielli 2000; Goldingay & Newell 2000; Ursenbacher et al. 2009; DiLeo et al. 2010). Conservation programs, however, almost completely ignore important co-evolutionary interactions, one of the most important being the antipredator strategies that have evolved to protect species from predation (but see Bonebrake et al. 2010). For example, vulnerable meadow vipers (*Vipera ursinii*) may gain beneficial protection against predation by exhibiting a dorsal zigzag pattern (a warning signal) that is similar to other vipers (e.g., adder [*Vipera berus*]) (Wüster et al. 2004; Kreiner 2007; Valkonen et al. 2011a). Even if adders were common in the area, a slight decrease in their population could substantially increase the predation mortality of meadow vipers.

Smooth Snakes and Adders in Åland

The smooth snake (*Coronella austriaca*) is a nonvenomous, medium-sized (up to 80 cm), and relatively slender Colubrid species, which is widely distributed across Europe. Its range reaches from the Iberian Peninsula to the Ural Mountains. Northernmost populations reach up to 60° N latitudes in Sweden and Åland (Arnold & Burton 1978; Kreiner 2007). This diurnal highly secretive species feeds mainly on lizards, but snakes and small mammals are consumed by larger individuals, whereas the smaller ones consume invertebrates (Arnold & Burton 1978; Goddard 1984; Luisielli et al. 1996). Females reach maturity in their fourth or fifth summer after reaching a length >40 cm, and the majority reproduce every second or third year by giving birth to 2–11 live young at a time (Spellerberg & Phelps 1977; Luisielli et al. 1996; Reading 2004). Smooth snakes can be found in various environments, but in the northern part of their range (Sweden and Åland) their typical habitat is relatively dry, open, and rocky hillsides. Populations of the smooth snake are often small, and

they are thinly scattered over the species range (Santos et al. 2009). Thus, the smooth snake is included in the list of specially protected species in the European Union (Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora, annex IV). The only known populations of the smooth snake in Finland are located in Åland islands, and the species is classified as vulnerable (Rassi et al. 2010), although its reclassification as endangered has been recently suggested (J.A. Galarza, unpublished data).

The adder (*Vipera berus*) is a venomous medium-sized (up to 90 cm) snake. It is widely distributed across central and northern Europe and Asia, reaching up to the Arctic Circle. Occurring from the United Kingdom to eastern Russia, it is the most widely distributed snake species (Arnold & Burton 1978). Adders are the only native reptile species not protected by Finnish law, and it is categorized as least concern on the Finnish Red List (Rassi et al. 2010). Like other European vipers (genus *Vipera*), the adder exhibits a characteristic dorsal zigzag pattern (see De Smedt 2001), which signals their secondary venomous defense to predators (Wüster et al. 2004; Niskanen & Mappes 2005; Valkonen et al. 2011a). Another common feature among vipers (family Viperidae) is their characteristic triangular-shaped head, which is also recognized and avoided by predators (Valkonen et al. 2011b).

Smooth snakes share only superficial similar dorsal patterning with the venomous adder (Fig. 1). When threatened by a potential predator, smooth snakes increase their resemblance (accuracy of mimicry) of vipers by flattening their heads and making its shape triangular. As the triangular head shape of vipers is recognized and avoided by predators, smooth snakes gain extra protection by displaying head flattening (Valkonen et al. 2011b). Smooth snakes are thus Batesian mimics of adders.

To provide a more qualitative illustration of frequency dependency of predation risk in the mimicry system, we revisited data published by Lindström et al. (1997). Experimental data provides the opportunity to obtain predation risk estimates when data from natural populations is not available. In their experiment, Lindström et al. (1997) tested how the abundance of model species in relation to the abundance of mimics affects the predation pressure on mimics. In their experiment conducted in controlled laboratory settings, they used a prey population consisting of three artificial prey species (model, mimic, and alternative prey) and wild caught Great Tits (*Parus major*) as a predator. They manipulated the frequencies of the unpalatable model and the palatable mimic while keeping the total size of the prey population and abundance of alternative palatable prey constant. Lindström et al. (1997) repeated their experiment with two palatability levels of the model species (for a detailed description see Lindström et al. 1997). They found that the survival of the mimic is dependent on the abundance of the model. To obtain an estimated predation risk for



Figure 1. (a) Venomous adder and (b) smooth snake mimic of the adder. To increase its resemblance (mimicry) to the adder, the smooth snake (c) has flattened its head in response to a potential predator.

Table 1. Generalized mixed effect model fitted with data from Lindström et al. (1997) to obtain predation risk estimates for model (species that is mimicked), mimic, and alternative prey relative to the abundance of the model species.*

Term to remove	df	AIC	$p \chi^2$
None		1108.1	
Palatability of the model	1	1109.8	0.054
Prey species* frequency of the model	2	1110.6	0.037

*Estimates are based on experiment with artificial prey species; therefore, we do not refer an exact prey type or species here; rather, we assume all mimicry systems are hunted by predators in a frequency-dependent manner. Model structure: $\text{attack risk} \sim \text{palatability of the model} + \text{prey species} + \text{frequency of the model} + \text{prey species} : \text{frequency of the model} + (1|\text{bird species})$.

each species (model, mimic, and alternative), we fitted a generalized linear mixed model with Laplace approximation to their data. Based on the results presented by Lindström et al. (1997), we included palatability of the model species, species (model, mimic, and alternative), frequency of the model species (in relation to mimic), and interaction between prey species and frequency of the model species as explanatory variables. Fate of individual prey (predated or not) was included as a binary response. To take into account the structure of data (repeated measurements within the predator), we used bird identity as a random effect in our model. Our starting model appeared to be the best fitting model (Table 1). Our model

showed that the benefits of mimicry were nonexistent at the point where the abundance of the mimic exceeded the abundance of model when overall predation on the prey species complex was expected to remain constant (Fig. 2).

Snakes are predated upon by birds of prey (e.g., Accipitriformes and Corvidae) and mammals (e.g., Mustelidae) (Cramp 1985; Selas 2001; Madsen 2011). Both mammalian and avian predators can learn and avoid the warning signals of snakes (e.g., Pfennig et al. 2001; Wüster et al. 2004; Valkonen et al. 2011a, 2011b). Furthermore, Pfennig et al. (2001) found evidence that the proportion of coral snake mimics attacked by mammalian predators increased when venomous coral snakes (the model) were absent. Thus, despite obvious differences in predatory behavior between Great Tits used in the laboratory experiment by Lindström et al. (1997) and natural predators of snakes, we believe that they are qualitatively similar in terms of selection of prey. However, in the experiment by Lindström et al. (1997), the phenotypic difference between model and mimic was small, whereas differences between smooth snakes and adders to raptors may be more obvious. In this scenario, one may expect smooth snakes to have higher predation than mimics in the experiment by Lindström et al. (1997).

Even though mimicry benefits the mimic by enhancing the probability that predators will misclassify them as a defended model and will not attack them (Caley

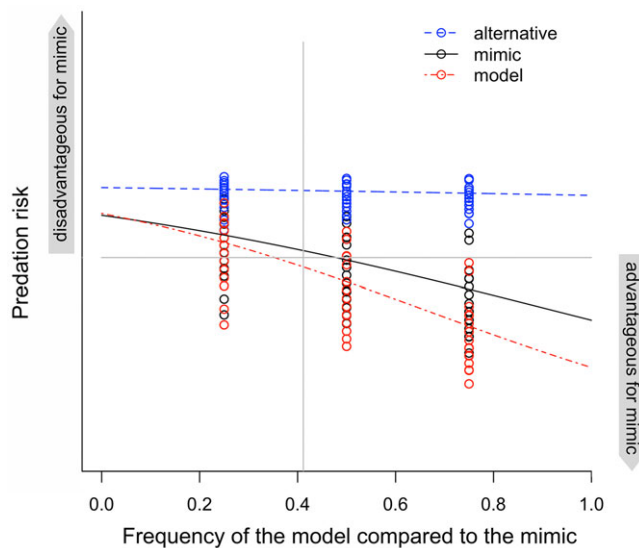


Figure 2. Predation risk estimates for a model species (i.e., a species that is mimicked), a mimic, and an alternative prey species relative to their frequencies (gray horizontal line, mean predation on prey population that is assumed to be constant and independent from model:mimic ratio; vertical grey line, model:mimic ratio has been estimated from effective population sizes of vipers and smooth snakes in Åland). Data are from Lindström et al. (1997).

& Schluter 2003), this may not hold true for human predators. Adders (like all vipers) are often abhorred and, especially if not protected by law, are frequently killed by people. We know of no systematic data on how frequently humans kill snakes. However, we have observed that even trained biologists often mistake the protected smooth snakes and other mimics for vipers. The IUCN Red List of European reptiles states that the deliberate persecution of reptiles is one of the major threats, in addition to habitat loss, pollution, and climate change, in Europe to these species (Cox & Temple 2009). Indirect evidence for humans killing snakes deliberately can also be seen in European museum collections, where a large number of the preserved individuals were killed by farmers (J.K.V., personal observation).

Effective population size (number of breeding females) of the smooth snake in Åland is estimated to be 41.35 individuals (J.A. Galarza, unpublished data), and Finnish law protects this species. We found that the adder population in Åland seems to be even smaller, although it is believed to be relatively common. Effective population size here is estimated as low as 28.93 individuals (J.A. Galarza, unpublished data). When the model:mimic ratio was estimated from the effective population sizes of vipers and smooth snakes in Åland it appeared to be alarmingly low: 0.41 (Fig. 2). That is below the threshold (0.48), considering

that the estimated predation risk of mimics exceeds the mean predation risk of the prey community. This highlights that the threats for snake populations in Åland are not well known, which is an impetus for further investigation. Both adders and smooth snakes are frequently found in residential, where they are exposed to human persecution. Therefore, for the successful conservation of smooth snakes in Åland, it seems crucial to also protect adders. This would ensure the effectiveness of the smooth snake's antipredator strategy of mimicry.

Other Systems and Future Directions

Mimicry is common among snakes (Brodie & Brodie 2004), and the global, substantial decline of snake species requires re-consideration of conservation actions for this group (Reading et al. 2010). Defensive mimicry (Batesian and Müllerian) is not limited to snakes. It occurs among a wide variety of taxa from invertebrates to vertebrates (Ruxton et al. 2004), and most likely all mimicry rings have not been discovered yet. Recognizing and considering the antipredator strategies of a species can lead to a substantial improvement in the probability of success of its conservation. Vast theoretical and experimental knowledge on the evolution of mimicry argues that co-evolutionary arms races should be considered carefully during conservation actions.

In Åland protecting the adder would prevent humans, though partly unintentionally, from further endangering smooth snakes. Cases when humans persecute model species are of course extreme. However, mimicry as an antipredator strategy is always dependent on the abundance (relative or absolute) of the other species that share the warning signals (Mallet 1999). Therefore, to achieve conservation goals, mimicry dynamics should be considered, among other ecological and evolutionary factors. Sometimes protecting the model among the mimics can be crucial for ensuring that the natural antipredator strategy (mimicry) of the target species remains effective. For example, one can assume, based on both theoretical and empirical evidence, that in Batesian mimicry (Bates 1862) models should be generally more common than mimics to ensure effectiveness of the mimicry (Cott 1940; Huheey 1964; Lindström et al. 1997). In Müllerian systems, the benefits gained by the less abundant co-mimic can be expected to decrease if the abundance of the common species decreases (Müller 1879; Joron & Mallet 1998; Mallet 1999; Honma et al. 2008). This suggests that conservation of even relatively common and abundant Müllerian co-mimics is needed if one of the species in the mimicry ring is endangered. For example, the endangered splendid poison frog (*Oophaga speciosa*), which shares similar red warning coloration with the more common strawberry poison frog (*Oophaga pumilio*), would likely be more protected from predation if the density of its co-mimic remained high. Furthermore, considering

the possible mimicry dynamics in the conservation of endangered species can cost-effectively help meet conservation goals.

Unfortunately, there are no data available that would quantitatively demonstrate the frequency dependent effect of predation on mimicry systems in natural populations. Therefore we are not able to present more concrete evidence of the extent of these interspecies relationships in which one of the two species is threatened. Instead, we encourage readers to consider this issue in the light of the extensive theoretical and experimental evidence available. Furthermore, our results provide foresight to prevent a potential disaster in a situation where a mimic becomes endangered due to the decreased frequency of its model species.

Acknowledgments

We are grateful for the Darwin Club and Journal Club of Ecology and Evolutionary biology division, L. Lindström, B. Rojas, R. Thorogood, S. Waldron, C. Lindstedt, S. Karek-sela, editor M. Burgman, and an anonymous reviewer for helpful discussion and insightful comments on the manuscript. Nätö biological station provided the facilities in Åland. Centre of excellent in Biological interactions (project SA-21000004745) funded the study.

Literature Cited

- Arnold, E. N., and J. A. Burton. 1978. A field guide to the reptiles and amphibians of Britain and Europe. Finnish edition Viitanen, P., P. Koskela, and E. Lindholm. 1981. Kustannusosakeyhtiö Tammi, Helsinki.
- Bates, H. W. 1862. Contributions to an insect fauna of the Amazon valley. Lepidoptera: Heliconidae. Transactions of the Linnean Society of London **23**:495-566.
- Beccaloni, G. W. 1997a. Ecology, natural history and behaviour of ithomiine butterflies and their mimics in Ecuador (Lepidoptera: Nymphalidae: Ithomiinae). Tropical Lepidoptera **8**:103-124.
- Beccaloni, G. W. 1997b. Vertical stratification of ithomiine butterfly (Nymphalidae: Ithomiinae) mimicry complexes: the relationship between adult flight height and larval host-plant height. Biological Journal of Linnean Society **62**:313-341.
- Berenbaum, M. R. 1995. Aposematism and mimicry in caterpillars. Journal of the Lepidopterists' Society **49**: 386-396.
- Bonebrake, T. C., L. C. Ponisio, C. L. Boggs, and P. R. Ehrlich. 2010. More than just indicators: a review of tropical butterfly ecology and conservation. Biological Conservation **143**:1831-1841.
- Brodie, E. D., and E. D. Brodie. 2004. Venomous snake mimicry, Pages 617-633 in J. A. Campbell and W. W. Lamar, editors. The venomous reptiles of the western hemisphere. Cornell University Press, Ithaca, NY.
- Caley, M. J., and D. Schluter. 2003. Predators favour mimicry in a tropical reef fish. Proceedings of Royal Society of London B. **270**:667-672.
- Cott, H. B. 1940. Adaptive colouration in animals. Methuen, London.
- Cox, N. A., and H. J. Temple. 2009. European red list of reptiles. Luxembourg: Office for Official Publications of the European Communities.
- Cramp, S. 1985. Handbook of the birds of Europe, the Middle East and North Africa, vol IV. Oxford University Press, Oxford.
- De Smedt, J. 2001. Die europäischen Vipern. Artbestimmung, Systematic, Haltung und Zucht. Johan De Smedt, Füssen.
- DiLeo, M. F., J. R. Row, and S. C. Loughheed. 2010. Discordant patterns of population structure for two co-distributed snake species across a fragmented Ontario landscape. Diversity and Distributions **16**:571-581.
- Filippi, E., and L. Luisielli. 2000. Status of the Italian snake fauna and assessment of conservation threats. Biological Conservation **93**:219-225.
- Goddard, P. 1984. Morphology, growth, food habits and population characteristics of the smooth snake *Coronella austriaca* in southern Britain. Journal of Zoology (London). **204**:241-257.
- Goldingay, R. L., and D. A. Newell. 2000. Experimental rock outcrops reveal continuing habitat disturbance for an endangered Australian snake. Conservation Biology **14**:1908-1912.
- Harper, G. R., and D. W. Pfennig. 2007. Mimicry on the edge: Why do mimics vary in resemblance to their model in different parts of geographical range? Proceedings of Royal Society of London B. **274**:1955-1961.
- Honma, A., K-I. Takakura, and T. Nishida. 2008. Optimal-Foraging Predator Favors Commensalistic Batesian Mimicry. PLoS ONE **3**. DOI: 10.1371/journal.pone.0003411.
- Hossie, T. J., and T. E. Sherratt. 2014. Does defensive posture increase mimetic fidelity of caterpillars with eyespots to their putative snake models? Current Zoology **60**:76-89.
- Huey, R. P., and E. R. Pianka. 1977. Natural selection for juvenile lizards mimicking noxious beetles. Science **195**:201-203.
- Huheey, J. E. 1964. Studies of warning coloration and mimicry. IV. A mathematical model of model-mimic frequencies. Ecology **45**:185-188.
- Joron, M., and J. L. B. Mallet. 1998. Diversity in mimicry: Paradox or paradigm? Trends in Ecology and Evolution **13**:461-466.
- Kreiner, G. 2007. The snakes of Europe: all species from West of the Caucasus Mountains. Chimaira, Frankfurt.
- Lindström, L., R. V. Alatalo, and J. Mappes. 1997. Imperfect Batesian mimicry—the effects of the frequency and the distastefulness of the model. Proceedings of Royal Society of London B. **264**:149-153.
- Luisielli, L., C. Capula, and R. Shine. 1996. Reproductive output, costs of reproduction, and ecology of the smooth snake, *Coronella austriaca*, in the eastern Italian Alps. Oecologia **106**:100-110.
- Madsen, T. 2011. Cost of multiple matings in female adders (*Vipera berus*). Evolution **65**:1823-1825.
- Mallet, J. 1999. Causes and consequences of a lack of coevolution in Müllerian mimicry. Evolutionary Ecology **13**:777-806.
- Mappes, J., and R. V. Alatalo. 1997. Batesian mimicry and signal accuracy. Evolution **51**:2048-2051.
- Müller, F. 1879. Ituna and Thyridia: a remarkable case of mimicry in butterflies. Proceedings of the Entomological Society of London **1879**: XX-XXIX.
- Niskanen, M., and J. Mappes. 2005. Significance of the dorsal zigzag pattern of *Vipera latastei* gaditana against avian predators. Journal of Animal Ecology **74**:1091-1101.
- Norman, M. D., J. Finn, and T. Tregenza. 2001. Dynamic mimicry in an Indo-Malayan octopus. Proceedings of Royal Society of London B. **268**:1755-1758.
- Pfennig, D. W., W. R. Harcombe, and K. S. Pfennig. 2001. Frequency-dependent Batesian mimicry. Nature **410**:323-323.
- Pfennig, D. W., and S. P. Mullen. 2010. Mimics without models: causes and consequences of allopatry in Batesian mimicry. Proceedings of Royal Society B. **277**:2577-2585.
- Poulton, E. B. 1890. The colors of animals. Trübner & Co Ltd., London.
- Rassi, P., E. Hyvärinen, A. Juslén, and I. Mannerkoski. 2010. The 2010 Red List of Finnish Species. Ministry of the Environment, Helsinki. (ISBN 978-952-11-3805-8).
- Reading, C. J. 2004. The influence of body condition and prey availability on female breeding success in the smooth snake (*Coronella austriaca* Laurenti). Journal of Zoology (London) **264**: 61-67.

- Reading, C. J., L. M. Luiselli, G. C. Akani, X. Bonnet, G. Amori, J. M. Ballouard, E. Filippi, G. Naulleau, D. Pearson, and L. Rugiero. 2010. Are snake populations in widespread decline? *Biology Letters* **6**:777–780.
- Ruxton, G. D., T. N. Sherrat, and M. P. Speed. 2004. *Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry*. Oxford University Press, Oxford.
- Santos, X., J. C. Brito, J. Caro, A. J. Abril, M. Lorenzo, N. Sillero, and J. M. Pleguezuelos. 2009. Habitat suitability, threats and conservation of isolated populations of the smooth snake (*Coronella austriaca*) in the southern Iberian Peninsula. *Biological Conservation* **142**:344–352.
- Selas, V. 2001. Predation on reptiles and birds by the common buzzard, *Buteo buteo*, in relation to changes in its main prey, voles. *Canadian Journal of Zoology* **79**:2086–2093.
- Spellerberg, I. F., and T. E. Phelps. 1977. Biology, general ecology and behaviour of the snake, *Coronella austriaca* Laurenti. *Biological Journal of Linnean Society* **9**:133–164.
- Symula, R., R. Schulte, and K. Summers. 2001. Molecular phylogenetic evidence for a mimetic radiation in Peruvian poison frogs supports a Müllerian mimicry hypothesis. *Proceedings of Royal Society of London B*. **268**:2415–2421.
- Ursenbacher, S., J.-C. Monney, and L. Fumagalli. 2009. Limited genetic diversity and high differentiation among the remnant adder (*Vipera berus*) populations in the Swiss and French Jura Mountains. *Conservation genetics* **10**:303–315.
- Valkonen, J., M. Niskanen, M. Bjöklund, and J. Mappes. 2011a. Disruption or aposematism? Significance of dorsal zigzag pattern of European vipers. *Evolutionary Ecology* **25**:1047–1063.
- Valkonen, J. K., O. Nokelainen, and J. Mappes. 2011b. Antipredatory function of head shape for vipers and their mimics. *PLoS One* **6**, DOI: 10.1371/journal.pone.0022272.
- Wüster, W., et al. 2004. Do aposematism and Batesian mimicry require bright colours? A test, using European viper markings. *Proceedings of Royal Society of London B*. **271**:2495–2499.