

Selective factors in the evolution of insect wings: response to Kukalová-Peck

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Kukalová-Peck (J. Kukalová-Peck. 1987. *Can. J. Zool.* **65**: 2327–2345) has recently criticized the hypothesis that selection for increased thermoregulatory capacity was important in the early evolution of wings from protowings. Here we argue that the current paleontological, embryological, and experimental evidence cannot be used to reject the thermoregulatory hypothesis. Experimental studies of aerodynamics and thermoregulation suggest that knowledge of the body size of ancestral pterygotes is crucial to evaluating the relative importance of aerodynamic and thermoregulatory factors in the evolution of flight.

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Kukalová-Peck (J. Kukalová-Peck. 1987. *Can. J. Zool.* **65** : 2327–2345) a récemment remis en question l'hypothèse selon laquelle la sélection vers une capacité thermorégulatrice accrue a joué un rôle important au début de la transformation évolutive des proto-ailes en ailes. Nous maintenons que les données paléontologiques, embryologiques et expérimentales actuelles ne permettent pas de rejeter l'hypothèse thermorégulatrice. Les résultats d'études expérimentales de l'aérodynamique et de la thermorégulation indiquent que la connaissance de la taille des ptérygotes ancestraux est essentielle à l'évaluation de l'importance relative des facteurs aérodynamiques et thermorégulateurs dans l'évolution du vol.

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In a recent review of the role of thoracic side lobes in the origin of insect wings, Kukalová-Peck (1987) discusses current evidence on selective factors in the evolution of flight. She sharply criticizes the hypothesis that selection for increased thermoregulatory capacity was important in the early evolution of wings from protowings, as proposed by Whalley (1979) and Douglas (1981) and investigated in detail by Kingsolver and Koehl (1985). Citing a recent study by Wootton and Ellington (1988), Kukalová-Peck revives (for discussion, see Hinton 1963; Wigglesworth 1976) the hypothesis that selection for increased gliding and (or) parachuting was central to the evolution of wings from protowings, whereby the insect would "jump from a high rock into rising air" (Kukalová-Peck 1987, p. 2342). Here we discuss how Kukalová-Peck (1987) has misinterpreted our work (Kingsolver and Koehl 1985) in several important regards, and discuss the relationship of our results to those of Wootton and Ellington (1988).

First, Kukalová-Peck states that "Kingsolver and Koehl's (1985) experimental model . . . fails to accommodate currently known biological evidence on mobility and seriality of protowings." Thus, she implies that our hypotheses are necessarily associated with a paranotal origin of protowings that are primitively rigid, whereby selection for thermoregulatory performance was important in the evolution of the functional articulation of the wing (p. 2342). This interpretation is incorrect: as we emphasized in our Introduction (p. 489) and Discussion (pp. 500–502), our experiments test hypotheses relevant to both rigid and moveable winglets. For example, the hypotheses we tested concerning attitude (roll) control require the existence of moveable winglets. Furthermore, Kukalová-Peck states (p. 2342) that we claim that "thermoregulation is of focal importance" in "instigating" the functional articulation of wings. This is incorrect: although we did

point out that the effectiveness of winglets as thermoregulatory structures is enhanced if the winglets are moveable (p. 502), we did not state that thermoregulation was important in the origin of the wing articulation. Kukalová-Peck also states that our model "uses only thoracic winglets" (p. 2342). This statement is incorrect for our thermoregulatory studies: we measured thermoregulatory performance of models with serial winglets on all abdominal and thoracic segments (e.g., Fig. 10 in our paper). We also measured the consequences of an extra (third) pair of thoracic winglets on aerodynamic performance, but when we found no effect (e.g., Fig. 7 in our paper) we did not continue adding winglets to the abdomen. Clearly, the thermoregulatory hypothesis has no necessary relationship to the paranotal hypothesis of wing origin.

Second, Kukalová-Peck uses evidence in favor of an aerodynamic hypothesis to conclude that the thermoregulation hypothesis is "improbable." This reasoning is logically flawed, because evaluation of such functional hypotheses for fossils can only be in the form of a plausibility argument. As we stated in our paper (p. 500), "At best, we can eliminate certain hypotheses as untenable and document other hypotheses as at least plausible." Evidence for one hypothesis is not evidence against another.

Kukalová-Peck's support for an aerodynamic hypothesis rests largely on an interesting recent study by Wootton and Ellington (1988). Kukalová-Peck (p. 2342) states that "Their results do not support the model of Kingsolver and Koehl," but this general statement obscures the many important similarities and differences between our results and those of Wootton and Ellington. The models of Wootton and Ellington differ from the ones we used in our aerodynamic experiments in several important respects. (i) Their models had twistable wings (i.e., the angle of attack of the wing could be made different from that of the body) on all segments of the thorax

and abdomen, whereas ours had rotatable wings (i.e., the up-down position of the wings could be altered) on the thorax; (ii) their models had cylindrical bodies that were 8 and 16 cm in length, whereas ours had insect-shaped bodies that were 2, 6, and 10 cm in length; (iii) they considered only a single short wing length, whereas we examined models with a wide range of wing lengths, including wingless models; and (iv) their models were dropped or gently thrown and the glide paths recorded, whereas ours were mounted in a wind tunnel and the aerodynamic forces on them were measured. Wootton and Ellington also measured an aspect of aerodynamic performance not addressed in our study: pitch stability. The principal results of Wootton and Ellington's study were that (i) winglets provided roll stability for both of their models and (ii) winglets adjusted to the appropriate angle of attack provided pitch stability and a good glide angle (equivalent to the lift/drag measured in our study) for their 16-cm model, but not for their 8-cm model.

Because of the importance of size and scaling for functional performance (Kingsolver and Koehl 1985), it is essential to compare the results of Wootton and Ellington with ours carefully. As Wootton and Ellington state, their results for their large model are equivalent to those for a 7-cm orthopteran of similar shape with a glide speed of 5.9–12.8 m/s. Such glide speeds are 50 to 320% greater than flight speeds measured on extant desert locusts (Jensen 1956), an orthopteran of similar size to that proposed, and they are much greater than values for any insect to our knowledge. In our wind tunnel studies, we used air speeds (glide speeds) of 1.0–4.0 m/s, covering the range of glide speed values reported for insects in the literature (e.g., Vogel 1981). In terms of Reynolds number, R_e (using for comparison body diameter as the characteristic dimension), Wootton and Ellington's model was operating at $R_e = 3267-7089$, whereas the maximum R_e values studied in Kingsolver and Koehl were $R_e = 1978-3165$. Thus Wootton and Ellington's results apply to larger sizes and higher air speeds than all but the largest model and highest air speed considered in Kingsolver and Koehl. We believe that a glide speed of 6–13 m/s is inconsistent with Kukalová-Peck's scenario of a large insect jumping from a high rock and "settling down to a soft landing" (p. 2342).

Kukalová-Peck (1987, p. 2342) states that Kingsolver and Koehl (1985) concluded that "small protowings could not have been used in flight." In fact, our results clearly showed that relatively shorter winglets can increase gliding performance as body size increases; indeed, the importance of size for performance was one of the two main points of our paper (see, for example, Fig. 11 in Kingsolver and Koehl 1985). For example, our results for lift/drag for the largest models we considered (10 cm long) suggested that "wings less than 1 cm long may have important effects" on gliding performance (p. 500). On the other hand, small winglets on smaller bodies did not improve aerodynamic performance relative to wingless models. In this sense, the results of Kingsolver and Koehl (1985) and of Wootton and Ellington (1988) are consistent: relatively shorter wings may have important aerodynamic effects as body size (Reynolds number) increases, and at very large body sizes (Reynolds numbers) quite short wings might be useful for gliding.

Our results also showed a change in flow patterns around the wings of our 10-cm models and a resultant lower absolute lift/drag than in the 6-cm models. In contrast, Wootton and Ellington observed an improvement in glide angle for their

16-cm model compared with their 8-cm model. It would be interesting to study the flow fields around their models to discover the mechanism responsible for these different results. Note that the decrease in absolute aerodynamic performance with body size that we observed in our 10-cm models did not occur for our measurements on parachuting or attitude control. However, natural selection for increased wing length on the basis of increased aerodynamic performance depends on the change in aerodynamic performance with changes in wing length, not on absolute performance. Unfortunately, Wootton and Ellington's study considered only a single wing length (in particular no wingless models were considered), and therefore cannot address this important issue.

It is clear that resolution of the question of the function(s) of wings during this transitional period depends on the body size of ancestral pterygotes; in particular, were ancestral pterygotes very large relative to extant insect groups? Ideas on the size of ancestral pterygotes continue to change. Wigglesworth (1976) suggested a body length of 1–2 cm. Kukalová-Peck, in a review of our 1985 paper, suggested a body length of 3–4 cm (J. Kukalová-Peck, personal communication, 1984). Both Kukalová-Peck (1987) and Wootton and Ellington (1988) suggest that ancestral pterygotes were quite large, but do not suggest a specific range or value. These suggestions are based on the fact that most insect fossils from the Middle Upper Carboniferous (Westphalian) are more than 2 cm in body length, and many are considerably larger (Kukalová-Peck 1987). However, pterygotes evolved at a much earlier date, probably during the Devonian. As Stanley (1979) points out, changes in body size are among the most common phyletic, macroevolutionary patterns found in the fossil record, so that inferring the size of ancestral pterygotes without direct fossil evidence from the transitional period in question may be difficult at best. The fact that one's answer to the question "What selective factors were involved in the early evolution of wings and flight?" depends critically on one's estimate of the size of ancestral pterygotes supports our suggestion (Kingsolver and Koehl 1985) that body size may have played a central role in the evolution of flight.

We do not understand why Kukalová-Peck (1987) criticizes our empirical study with the statement "mathematics is *not* a solution by itself to the origin of insect flight" (p. 2342, italics in original). Nonetheless, we wholeheartedly agree with Kukalová-Peck's statement that "the only way to approach the question of the origin of insect wings is by the *integrated, simultaneous consideration of all available evidence*" (p. 2342, italics in original). Surely empirical measurements of the performance of models of fossil organisms, like those of Kingsolver and Koehl (1985) and Wootton and Ellington (1988), provide useful data to complement the paleontological and biological evidence being used to piece together the puzzle of the origins of flight.

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