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RICTAL BRISTLE FUNCTION IN WILLOW FLYCATCHER

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ABSTRACT.—We examined the function of rictal bristles on Willow Flycatchers by testing whether their removal or the placement of small pieces of transparent tape on them would reduce the ability of captive birds to capture live house flies. Neither operation adversely affected the birds' ability to capture prey, indicating that the rictal bristles do not aid in prey capture. Other experiments with bird specimens placed in a wind tunnel demonstrated that rictal bristles may protect the eyes from food items the bird is trying to capture. Particles released in front of the bird's open mouth and blown back towards its head struck an eye more frequently after the rictal bristles had been removed.

Much speculation has centered on the function of rictal bristles, stiff whisker-like feathers arising from the rictus and the margin of the feathered skin behind the horny covering of the upper mandible. Some authors have suggested that rictal bristles may serve as mechanoreceptors (Wallace 1955, Pettingill 1970) or chemoreceptors (Jany 1955). Dyer (1976) proposed that in birds that feed on large and potentially dangerous insects, such as bees and acridid grasshoppers, these bristles protect the eyes from the preys' legs and stingers. Other authors, noting that rictal bristles are common among insectivorous birds, have proposed their utility in capturing prey, possibly serving as an insect net or funnel (Welty 1962, Van Tyne and Berger 1976). Even if true, this cannot be their sole function, however, because rictal bristles are also found on many noninsectivorous birds (Stettenheim 1973).

Evaluation of these hypotheses has been hampered by the lack of experimental data. Lederer (1972), however, used high speed photography to show that the Great Crested Flycatcher (*Myiarchus crinitus*), Eastern Phoebe (*Sayornis phoebe*), and Eastern Wood Pewee (*Contopus virens*) usually catch flesh flies (*Sarcophaga bullata*) with their bill tips. From this, he suggested that rictal bristles perform no function in prey capture. However, when a bird misses its prey with its bill tip, rictal bristles may still serve to deflect the missed prey into the bill. They may also allow the bird a second strike opportunity by impeding the insect's escape or serving as mechanoreceptors that signal the missed prey's new location. Another hypothesis, owing to the rictal bristles' location between the eyes and mouth, is that these feathers may prevent escaping prey or parts of captured prey from hitting the bird's face and eyes.

We examined whether rictal bristles aid the Willow Flycatcher (*Empidonax traillii*) in prey capture or help protect the eyes. In our experiments, we manipulated the rictal bristles on specimens and observed whether there was any change in the birds' ability to capture prey or in the number of objects striking the eyes.

METHODS

Ten Willow Flycatchers were captured with mist-nets during July and August 1977 and 1978 at the Hudson Biological Reserve near Pullman, Washington. Each bird was housed separately in a 1.5 × 1.8 × 2.5 m screened cage and fed ad libitum a variety of live insects. Lighting during all tests was by overhead fluorescent and incandescent lights, which provided approximately 250 lux. All tests were conducted 5 to 15 days after a bird's capture.

Each bird was observed at a distance of 2 to 3 m as it captured live house flies (*Musca domestica*), first during a control period and then during one or two experimental periods. The first experimental period lasted one day while the control and the second experimental period lasted two to three days. To guard against the possibility that capturing and handling the birds during the experimental procedures might have been an important variable, all birds were similarly captured and handled prior to the control period.

We assumed that small objects placed on the tips of the rictal bristles to increase their length, weight, and wind resistance might temporarily disrupt their functioning if the bristles aid in prey capture by serving as mechanoreceptors. To test this, we removed each bird from its cage at the beginning of the first experimental period and folded a 2 × 2 mm piece of transparent adhesive tape over the end of a bristle. Two randomly selected rictal bristles on each side of each bird's head

TABLE 1. Capture success ratio of flycatchers when their rictal bristles were left intact, taped or removed.

	Control		Bristles taped			Bristles removed		
Specimen	Number attempts	Success ratio	Number attempts	Success ratio	χ^2 (vs. control)	Number attempts	Success ratio	χ^2 (vs. control)
Sally-gleaning attempts								
A	40	0.85	41	0.80	0.06	47	0.77	0.51
B	35	0.89	19	0.89	0.14	45	0.82	0.22
C	60	0.82	43	0.79	0.01	55	0.91	1.35
D	50	0.56	—	—	—	48	0.77	3.98*
E	75	0.87	—	—	—	91	0.84	0.12
Aerial hawking attempts								
A	24	0.92	21	0.81	0.38	24	0.92	0.27
B	18	0.89	10	0.90	0.30	23	0.78	0.23
C	51	0.78	49	0.78	0.002	44	0.77	0.01
D	72	0.65	—	—	—	25	0.92	5.33*
E	39	0.69	—	—	—	38	0.89	3.64

* $P < 0.05$.

TABLE 2. Effect of taping or removing the rictal bristles on the ratio of capture attempts with multiple bill snaps to those with a single snap.

	Control		Bristles taped			Bristles removed		
Specimen	Number attempts	Double snap ratio	Number attempts	Double snap ratio	χ^2 (vs. control)	Number attempts	Double snap ratio	χ^2 (vs. control)
A	61	0.05	65	0.09	0.35	75	0.05	0.08
B	48	0.07	18	0.06	0.22	63	0.09	0.08
C	79	0.08	62	0.07	0.10	68	0.10	0.08

were taped, after which the bird was returned to its cage.

If rictal bristles aid in catching prey, removing or cutting them off should also reduce a flycatcher's ability to catch insects. We tested this in the second experiment by cutting off the bristles at the skin line so that they no longer projected above the contour feathers. Three birds were tested during the first experimental period, and these same individuals plus two others were then tested during the second experimental period.

During the control and experimental periods, we recorded the number of attempts each bird made to capture flies by either aerial hawking or sally-gleaning and the proportion of successful attempts (capture success ratio). The ratio is a conservative estimate of capture success. House flies were used as prey because their small size, speed and maneuverability tested the flycatchers' capturing ability, and emphasized any decrease in this ability. Each bird's capture success ratio during each experimental period was compared to the ratio obtained during the control period using a 2 × 2 contingency table corrected for continuity.

A flycatcher sometimes made an audible snap as it rapidly closed its bill during a capture attempt. It usually snapped only once during a capture attempt but occasionally made two or more snaps as it struck repeatedly at the same fly. The ratio of multiple snaps to single snaps was determined for three of the birds during each of the control and experimental periods, and then compared using a 2 × 2 contingency table corrected for continuity.

To test whether rictal bristles shield the eyes from items a bird is trying to eat we placed six preserved flycatchers, fixed with their mouths opened 1–2 cm, in a wind tunnel and then simultaneously released 10 to 20 pieces of wood or plastic 0.2 to 2.0 mm in length from a fixed position 1–3 cm in front of each bird's mouth. The birds were held in position by a rod that exited from the rear of the bird's body and connected to the back of the wind tunnel. The wind speed was 5 m/s. The directionality of the rictal bristles was not changed or controlled on any specimens. To measure the frequency of items striking the eyes, we put adhesive discs over the eyes so that any striking objects would adhere to them. The eye disc protruded 1–2 cm above the surface of the face. The number of adhering particles was then counted. Each specimen was tested in this manner 10 times and the results totalled for each specimen. The results for each specimen were then statistically compared using the chi-square test to determine whether the number of particles striking each side of the bird's face significantly differed from one another. The rictal bristles on one side of the specimen were then cut off and the experiment repeated. These data were again totalled for each specimen and statistically analyzed.

RESULTS

Small pieces of tape on the ends of the rictal bristles apparently did not disrupt the birds' ability to capture flies because there was little change in capture success ratio for aerial hawking or sally-gleaning attempts by any of the birds (Table 1). Removing the bristles also did not reduce the ability of any of the birds to capture flies (Table 1). In fact, one bird had a significantly higher capture success ratio after its rictal bristles were cut off.

The ratio of capture attempts in which the birds made multiple snaps to those in which it made only a single snap did not change significantly during the control and experimental periods for any of the birds (Table 2). This indicates that neither cutting off nor taping rictal bristles altered the birds' ability to rapidly snap again at missed prey.

Before the bristles were removed, the number of particles adhering to the adhesive discs overlying the birds' eyes differed significantly in only one of the six specimens (Table 3). After the bristles were cut from one side of each bird's face, however, particles hit the discs on that side significantly more often in all six specimens (Table 3).

TABLE 3. Ratio of particles adhering to eye discs before and after the rictal bristles were removed from one side of the bird's head (experimental side).

	Before bristles removed			After bristles removed		
Specimen	Number particles	Ratio experimental to control side	χ^2	Number particles	Ratio experimental to control side	χ^2
AA	251	1.11	0.67	362	1.81	29.9**
BB	98	0.92	0.16	123	1.73	8.85**
CC	143	1.13	0.57	166	1.96	17.57**
DD	141	1.52	5.96*	136	1.61	7.52**
EE	181	1.03	0.05	275	1.55	12.66**
FF	183	0.87	0.92	194	1.49	7.44**
Total	997	1.08	1.37	1,256	1.68	81.53**

* $P \leq 0.05$.
** $P \leq 0.01$.

DISCUSSION

Lederer (1972) showed that the Great Crested Flycatcher, Eastern Phoebe and Eastern Wood Pewee capture flesh flies with their bill tips so that the rictal bristles could not function to funnel insects into the mouth. Our results, using a different species of flycatcher, different prey species, and different experimental conditions, agree with his findings that rictal bristles do not function as insect funnels and further failed to support any of the other prey-capture hypotheses. Taping several rictal bristles to increase their length, weight and wind resistance had no effect on prey-capture success. While this suggests that rictal bristles do not aid in prey capture by serving as mechanoreceptors, it is possible that the taping simply did not disrupt their functioning as mechanoreceptors. However, regardless of how rictal bristles function, their removal would be expected to reduce the proportion of successful capture attempts if they aided in prey capture. No significant reduction was evident for any of the experimental birds. Likewise, if the rictal bristles serve to increase the birds' ability to restrike rapidly at missed prey, removing them should also have decreased the frequency of multiple snaps, but no decrease was evident.

Rictal bristles might prevent food items from striking the eyes, as might happen when the prey is missed or breaks apart on capture. The results of the wind tunnel experiment support this possibility. The mean distance between individual bristles in 40 specimens of Willow Flycatcher that we examined was 1 mm. Hence, rictal bristles in this species probably are most efficient at stopping particles larger than 1 mm in diameter. These bristles may also help keep smaller particles out of the eyes by diverting the air flow away from the face.

The bristles' location, around the rictus instead of the eye, seems unusual if a primary function is to protect the eye. Some birds, indeed, do have bristles around the eyes that apparently serve as eyelashes (Stettenheim 1973). Why then should flycatchers and other birds have them only on the rictus? Probably in any bird the number, size, and location of bristles to protect the eyes is determined by evolutionary pressure resulting from the conflicting needs to protect the eyes and yet obtain an adequate field of vision. For birds that are likely to be hit by particles during normal flight or by particles coming from any direction, bristles immediately around the eyes are the only way to protect the eyes. In Willow Flycatchers, however, danger to their eyes probably arises chiefly from attempts to capture prey that can move unpredictably in escaping or are likely to break apart on capture. The location of bristles on the rictus should block any prey parts coming from the bill and still allow a clear forward field of view and in all other directions except downward. For instance, when chasing prey, the rictal bristles start to block the bird's view only after the bill tip reaches the insect.

Besides protecting the eyes, the rictal bristles may protect the feathers on the face from becoming soiled by food items. Possibly the short bristles along the lower bills of many flycatchers serve a similar function.

While our results failed to support any of the prey-capture hypotheses, they do not and cannot prove the null hypothesis—that rictal bristles do not aid in prey-capture. Furthermore, our findings do not exclude the possibility that rictal bristles aid in prey capture in other birds or even in other tyrant flycatchers, owing to the latters' diverse food habits and capture techniques (Fitzpatrick 1980). We can understand the functions of rictal bristles only after experimental studies have been conducted on many bird species using different types of prey.

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