

STUDIES IN SEXUAL PHENOMENA.

VIII. "TRANSFERENCE" AND ECLIPSE PLUMAGE IN BIRDS.

By J. M. WINTERBOTTOM, B.Sc.

In a previous paper of this series (1), I have discussed the significance of the transference of secondary sexual characters from male to female and, in less usual cases, from female to male. I then summed up the matter by suggesting that:

Owing to the less expensive gonads of this sex, many mutations are limited in expression to male animals; if these are of value in impressing the female or in overcoming other males, they will tend to be conserved, as suggested by the theory of Sexual Selection (of course, if the mutation was of use to the animal in its ordinary life, it would also tend to be preserved); in time, some mutation in the female may allow of the expression of these characters in her also, and here again, if they are of value, owing to the existence of mutual selection, they will tend to be preserved; the whole process is sifted through the sieve of Natural Selection which may eliminate a character at any stage in the process (p. 384).

In this previous paper, I gave instances of the evolution of sexual dimorphism within a genus and even within a species. A similar case of great interest is given by Bates (2). In the barbet *Tricholaema hirsutum*, four subspecies are recognised. In *T. h. flavipunctatum* (Main African forest, west to Cameroon), the sexes are alike. In *T. h. chapini* (northern edge of the forest, west to Lagos) and *T. h. hybridum* (Niger delta), the throat in the male tends to have more black and less white than in the female. In the typical *T. h. hirsutum* (Gold Coast, Ivory Coast, Liberia), the male has a black throat, while the female's throat is white streaked with black, as with both sexes of *T. h. flavipunctatum*. Here we see sexual dimorphism as it were in the act of evolution. The black throat is, in this species, a character acquired by the male and not expressed in the female; *i.e.* what I have called an *arctic* character.

In the paper already referred to, I gave many instances of "transference" (as we may call it, for short) from various groups of the animal kingdom. The following additional ones will serve here as examples of this widespread phenomenon.

Ogilvie-Grant (10) notes that in the painted francolin (*Francolinus pictus*), neither sex has spurs; in most species (*e.g.* the African *F. bicaratus*), the males have these weapons; while in a few (*e.g.* Hildebrandt's francolin), the females possess them as well. In pheasants (Ogilvie-

Grant, *loc. cit.*), only the males normally have spurs; but the female of the painted spur fowl (*Galloperdix limulata*) has one pair, as against the two to three pairs of the male, while in the fire-backed pheasants (*Acomus*), the females resemble the males in armature. In the notation previously adopted (Winterbottom, *loc. cit.*), most pheasants are: ♂, *M* (arctic); ♀ *N* (non-sexual); *Galloperdix* is: ♂, *M*; ♀, (*M*) (partially arctic); *Acomus* is: ♂, *M*; ♀, *M*.

In Rowland Ward's *The Sportsman's Handbook*(11), it is stated on the authority of R. J. Cunningham that one race of the klipspringer (*Oreotragus saltator schillingsi*) is distinguished by the presence of horns in the female as well as in the male.

Darwin(13) notes that the female *Ephippiger vitium* possesses stridulating organs very similar to those of the male. The same authority quotes Brauer on a curious case of dimorphism in certain species of the dragon-fly genus *Neurothemis*. Here, the females usually have ordinary wings, while the wings of the males are "very richly netted." But in some species some of the females have netted wings. A parallel case occurs in the genus *Agrion*, where some of the females are orange; this Darwin calls "probably a case of reversion," since orange or yellow is the usual female colour in the Libellulæ, when the sexes differ. The series therefore probably is:

Normal Libellulid, ♂, *M*; ♀, *N*.

Abnormal *Agrion*, ♂, *M*; ♀, *M* and *N*.

Normal *Agrion*, ♂, *M*; ♀, *M*.

Another case noted by Darwin concerns the orange-tip butterflies. In the British *Anthocharis cardamines*, the orange wing tip is confined to the male; in the Californian *A. sara*, the female has it also, though it is lighter in colour in this sex; in the related *Iphias glaucippe*, from India, this decorated tip is equally developed in both sexes.

The following cases are also taken from Darwin. In the rays (*Raia*), there may be sexual differences in the teeth. In many species the teeth are flat in both sexes, but in *R. clavata* the male has pointed teeth, as have both sexes of *R. batis* and *R. maculata*. The temporary crests of breeding male blennies may be transferred to the females; as may the crests of *Iguana*. In the lizard *Anolis cristatellus*, the male has a red throat pouch, which is represented by a rudiment in the female; in the female *Sitana*, even this rudiment is absent; whereas in other forms, both sexes possess a fully developed pouch. In the Asiatic elephant, tusks are normally absent in the Ceylon race, present in the males of

the continental form. In the African elephant, both sexes have tusks, although they are smaller in the female than in the male.

While it is difficult to get anything of value from Gould's turgid rhapsodies and dull discussions of synonyms, it would appear from his *Monograph* (15) that cases of transference occur in the humming birds. In all but one of the species of *Lampornis*, the male is brighter than the female, but in *L. porphyryrus* the two sexes are very similar. In most species of *Eriocnemis*, the two sexes are equally, or almost equally, decorated, but in *E. vestitus* the female is less brilliant, while in *E. nigrivestis* the male is black, the female green-bronze.

In the frigate birds (*Fregata*), both sexes of the Ascension frigate bird (*F. aquila*) resemble the males of the magnificent and great frigate birds (*F. magnificans* and *F. minor*) in being entirely black, whereas the females of these latter two species have the underparts white (see Alexander (17)).

In the peacock (*Pavo cristatus*), only the male has spurs, but in the Java species (*P. muticus*), spurs are present in both sexes.

As a final example, let us consider the development of the black head in the West African species of *Ploceus*¹. The account here is based on the descriptions given by Bates (2).

Ploceus aurantius has not a black head in either sex, though the male is brighter in colour than the female.

P. melanogaster has a black throat in the male. The rest of the plumage is black, however. (Cf. the albino drakes cited by the writer (1) in a previous paper.)

P. ocularius male has a black eye stripe and throat and the female also has the eye stripe. The rest of the plumage of the head is yellow or yellowish brown.

P. brachypterus male resembles the last but the head is brownish yellow.

P. baglajecht male has a small black mask.

P. heuglini, *P. luteolus*, *P. monachus* and *P. vitellinus* all show a black mask in the breeding male.

P. castaneofuscus, *P. nigerrimus*, *P. cucullatus*, *P. capitalis* and *P. melanocephalus*. The head of the breeding male in all these species is black.

¹ Many systematists distribute the birds here referred to amongst several genera, but I agree with Bates that the group "cannot be further subdivided without violent cutting of connections"—to say nothing of the disadvantage of such a method of nomenclature to the ordinary zoologist, who is thus compelled to remember three or four names, some of remarkable cacophony, instead of one.

P. tricolor, *P. albinucha* and *P. maxwelli* have black heads in both sexes.

The following species do not fit into the regular series but seem to be side-branches, as it were:

P. bicolor, in which the head is brown-black in both sexes.

P. dorsomaculatus in which both sexes have yellow on the top of the head; the throat of the female is black only at the sides.

P. anochlorus, in which the mask, not above the eyes, is black in both sexes. In the male, the top of the head is yellow, in the female black and olive. Here the female seems to be more arctic than the male.

But there is another series beyond the *P. tricolor* stage. In all the species so far considered the juvenile has been non-sexual; *i.e.* has not had a black head. In at least two of the species in the next series, the juvenile has a black head.

P. insignis. The top of the head of the male is dark chestnut, the throat black. In the female, the whole head is black.

P. preussi, *P. nigricollis* and *P. pachyrhynchus*. Head golden brown in the male, black in the female; throat dark in both. In *P. nigricollis* and *P. pachyrhynchus* at least, the juvenile has a black head.

P. batesi differs in that the head of the male is chestnut.

Fig. 1 represents the whole series diagrammatically. It should be borne in mind that this figure refers only to the state of the head and is not intended to be an evolutionary tree of the genus.

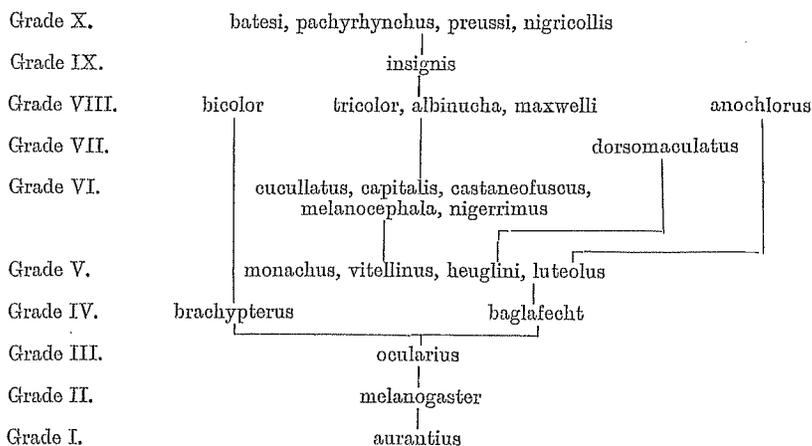


Fig. 1. Diagram showing the development of the black head in the West African species of *Ploceus*.

It might, of course, be argued that in this second series the black head is an aphyroditic¹ character and not an arctic one, but apart from the inherent improbability of the female evolving display characters more strongly than the male—a feature only shown in about three groups of birds—we have the very important evidence of the eclipse plumage. Those weavers that live in the grass and tree savannah zones have a definite and well-marked breeding plumage and in the non-breeding season they are much less conspicuous. This is the case with *P. luteolus* and *P. capitalis*, for instance. In the forest species, however, there is no eclipse plumage, using this term to include all specialised plumages which differ markedly from that assumed in the breeding season. Unfortunately all species of the second series except *P. pachyrhynchus* have no eclipse plumage. In *P. pachyrhynchus*, both sexes go into eclipse and in this plumage the head is blackish. In no case does the female alone go into eclipse, as she presumably would in the second series if the black head were an aphyroditic character. It will be recalled that only the female of the New Zealand sheldrake (*Casarca variegata*) goes into eclipse (see, e.g., Finn (3)). Moreover, the male would not assume an aphyroditic character in *eclipse* plumage.

This question of eclipse plumage has not yet been seriously attacked by physiologists. We know almost nothing of the liberating stimuli and physiological conditions of this stage. Beebe (4) has shown that for the American cardinal (*Cardinalis virginianus*), the liberating stimuli include the length of daylight and, perhaps, food, while experiments by Rowan (18) on *Junco hyemalis* show that gradual increase of the hours of daylight cause increase in the size of the gonads and promote migration. But the length of daylight, at least, is not very likely to be a controlling factor in the case of the West African weavers. The following hypothesis may be found useful:

We know that in birds in which the male is the more decorated sex, ovariectomy leads to the assumption of male plumage, while castration, in normal cases, has no effect. In ducks, however, castration leads to the permanent retention of the full breeding plumage². This is described in detail by Goldschmidt (5) and others. Further, cases of male-feathered but functionally normal females of the domestic fowl have been explained by Crew (6) on the assumption that the ovary was passing through

¹ A character acquired first by the female, I have called an aphyroditic character (Winterbottom (1)).

² But cf. Goodale (22, pp. 15–16) who records the case of a castrated *duck* which went into eclipse.

a resting period of unusual profundity at the time of moult. Again, the hen-feathering of the males of such breeds as the Sebright bantam has been explained on the assumption that the testis is, physiologically, expensive, and thus approximates to an ovary in the demands it makes upon the body. It is possible that growth rate and differential development are involved. If the male has the more rapid growth rate, it will finish the development of its primary sexual organs in time to devote the rest of the growing period to the elaboration of the secondary sexual characters. Although I do not know of any evidence to support this last, it is obvious that the same result would be achieved by prolonging the growth period of the male beyond the time at which sexual maturity is achieved, and of this there is abundant evidence, both in man and in the lower animals. Against this, however, we must set the fact that the same is true of females, at least in mammals. It is possible that, in polygamous mammals and in some birds, the partial or complete prevention of the young males from breeding, owing to the rivalry of their fully matured fellows, may have some effect on the development of secondary sexual characters. It would be an interesting experiment to take two groups of young male deer, allow the members of one group regular access to as many females as possible from the first, while keeping the second group celibates: and to see if there were any significant differences in the rate of antler growth between the two groups.

It may be that in the open country weavers (*Ploceus*), the strain of the breeding season saps the resources, and that they are sufficiently sensitive to such strains for this to inhibit the development of male plumage in the moult that immediately follows. It will, of course, be pointed out that the forest weavers do not react in this way. But food is more plentiful in the forest, so that the strain will not be so great.

That there is some such balance between the metabolic exchange of the gonad and that of the rest of the body is shown by the fact that the implantation of extra testicular tissue into the male causes the female plumage to be assumed.

Although the suggestion that the implantation of extra testicular tissue into a male causes the male gonads to become as "expensive" as the female is considered the most likely explanation, this view is not without its difficulties. Greenwood and Blyth (20) found that implanted testicular tissue in a female hindered the development of the oviduct and of the springiness and wide separation of the bones of the pelvis. This suggests the influence of a testicular hormone similar to that found by Lillie (21) and others to have such effect in the development of the

mammalian freemartin. But Greenwood and Blyth argue that the results of the removal of one testis and of partial ovariectomy point to the existence of a balance between the bulk of the gonadic tissue and that of the ordinary soma. They are inclined to attribute their own results to the underdevelopment of the ovary consequent upon the presence of extra, non-ovarian, but gonadic tissue in the body. These are not the only alternatives, however. For instance, it may be that the male condition of the pelvis, like the female type of plumage, is more "economical" than that of the opposite sex: extra gonadic tissue caused the assumption of this condition to "balance the books." Again, it may be that Crew's birds did not have time to reduce the bulk of their gonad before the moult supervened.

But, returning to releasing stimuli, the argument that food supply is responsible is not, I confess, a very strong one. A more likely supposition is that humidity and/or altitude are the liberating stimuli. That humidity has a marked effect on animal coloration is well known, and the variations in humidity in the open country are much greater than they are in the forest. In this connection it is worth noting that *Ploceus cucullatus*, the most abundant and widespread of the West African species of its genus, goes into eclipse in the north, but not in the forest country to the south.

It might be worth while mentioning a few examples of the effect of the humidity of the forest on colour. I shall confine my attention to West African birds. There are two races of the palm swift (*Cypsiurus parvus*), the one in the forest (*C. p. brachypterus*) being darker than the typical one. In the forest race of the giant kingfisher (*Ceryle maxima sharpei*), the white spots on the head and back are small or absent and there is more black on the underside. The head of the Senegal kingfisher (*Halcyon senegalensis*) is darker grey-brown in the forest subspecies (*H. s. fuscopileata*). The grey flycatcher of the forest (*Alseonax cassini*) is darker than its open country representative, the swamp flycatcher (*A. a. aquaticus*). The forest grass warbler (*Cisticola erythrops*) is brownish buff below, with "only the middle white" (Bates (2)), while the very similar whistling grass warbler (*C. lateralis*) of the savannah is "mostly white" on the underside. In *Prinia mistacea*, the type race is lighter than its forest representative (*P. m. melanorhynchus*) and the same is true of *Cameroptera b. brevicaudata* and *C. b. tincta*. The common open country drongo (*Dicrurus adsimilis*) has whitish quill linings on the underside of the wing, whereas the forest *D. atripennis* is wholly black; the iris is darker in the forest bird, too. A conspicuous exception to the

general rule that forest birds are darker than their open country representatives is found in the genus *Petrochelidon*, where *P. preussi*, the open country form, is blacker than *P. fuliginosa*. Altitude has the same effect as forest, as will be seen by the following quotation from Bannerman (12): "When the mountain birds are representative of species that occur at lower levels, it is the birds from the high, cold damp altitudes that are always darker in colour" (p. xli).

But while humidity may be the releasing stimulus, I feel convinced that it is the need for protective coloration which is at the root of the matter and which, by selection, has produced the condition we now see. In the forest, even the most brilliantly coloured bird is difficult to see—how difficult it is not easy to realise without first-hand experience. I have heard a bird calling not more than four feet away from me in a patch of dense second growth in Ashanti and all I saw was a movement of the leaves at the end of a branch as it took alarm. This was exceptional, but even in older forest, one can rarely see twenty yards and nothing like as far as that in the canopy or below about four feet. Moreover, the field is obstructed by leaves and branches and the light is dim and often flecked with little shafts of sunlight that dazzle the eye. Need for protective colouring is therefore not very great. In this connection, we see that most of the very highly decorated birds are forest dwellers—*e.g.* birds of paradise, peacock, golden and Amherst pheasants, etc. (Nevertheless, it is worth noting that the wild jungle fowl (*Gallus gallus*) goes into eclipse, a feature lost by its domestic descendant.) Of the golden pheasant (*Chrysolophus pictus*) in open country, Beebe (7) says that he never had any difficulty in detecting the males, which invariably made for cover as soon as they saw him. At the same time, in the West African savannahs, the need for protection is not equally urgent at all seasons. During the rains, when the grass is high, there is fair cover and this is when the birds breed. Moreover, in the case of colonial breeders like *Ploceus cucullatus*, it may be doubted whether protective coloration would be of much use—it certainly would not conceal the nesting colony, the noise of which by itself would betray it to any enemy that came at all near and the actual nests are usually visible long before the birds. But in the dry season, especially when the grass is burnt off, the need for protective coloration is more urgent, since most of the cover has disappeared. In those weavers which do not breed in colonies, such as *Euplectes* and *Colinus passer*, there is a further reason that may have influenced the development of bright colours. I have elsewhere suggested (8) that these birds may resemble many temperate species, such as

warblers and finches, in establishing and maintaining a breeding territory. Now, as Howard has shown (9), song is used by territorial species as a means of warning off other males and of advertising to the females the presence of a breeding male. Neither *Euplectes* nor *Colinus passer* has at all a loud voice and it may be that the bright colouring takes the place of song, for Nicholson (19) has pointed out that the volume and persistency of utterance of a song bears some relation to the conspicuousness or otherwise of the songster. Both *Euplectes* and *Colinus passer*, during the breeding season, constantly perch in conspicuous places. If this suggestion be confirmed, it is an interesting vindication (only partial, it is true) of the old traditional view that song and plumage are alternatives. The fact that Allen (16) in Liberia independently came to the same conclusions as the writer strengthens the probability of its being true.

It would seem, then, that eclipse plumage is assumed by male birds very largely for the purpose of protection, though the liberating stimulus may be humidity, altitude or length of daylight, or very possibly some other, unsuspected agent.

We must now consider why it is that the female does not assume the same plumage as the male for the breeding season. In the Anatidae, I believe that this is due primarily to the need for protection when incubating: a point that is confirmed by the fact that in the sheldrake (*Tadorna tadorna*) and the swans, for instance, where both sexes incubate, the male and female are similarly coloured. The sheldrake nests in burrows where its conspicuous colours are not seen, while the swans are probably large enough and strong enough to look after themselves.

But this cannot be the explanation in the weavers, all members of which family build domed nests, so that the plumage of the female cannot affect the issue. Here it is probably merely because suitable variations have not arisen in the females. When they have, and when protective colouring is important, we see that the female goes into eclipse just as the male does (e.g. in *Ploceus pachyrhynchus*). So that when an arctic nuptial plumage is transferred to the female, the double moult, with its accompanying eclipse plumage, is transferred as well. It is perhaps the need for this double transference that has limited the occurrence of arctic females to a few species.

One extremely strange set of facts does not readily fit into the generally accepted theory of eclipse plumages, however. In most ducks and in the weavers, the difference between the brilliant breeding plumage and the dull eclipse plumage is very striking and it is with such examples that we have hitherto been concerned. But a double moult from a nuptial to

an off-season dress and back again is not confined to such birds. Notably amongst the waders, the breeding plumage¹, though richer than the eclipse dress, cannot be looked upon as conspicuous. Moreover, we can construct a series in which the length of time before the nuptial plumage is renewed is progressively reduced, until we come to a state where the two plumages actually overlap and the breeding plumage begins to develop before the eclipse dress is fully grown. The only explanation that I can think of to cover the facts is to assume that the breeding plumage of such birds was once considerably more conspicuous than it is now and that the double moult was evolved to meet this contingency; with the change of breeding plumage, the double moult is gradually being eliminated and will finally disappear, since it subjects the bird to an unnecessary strain on its resources. A theory involving the recent development of protective coloration is not entirely unprecedented, for Pycraft⁽¹⁴⁾ has advanced something of the kind to account for the relatively bright plumage of young warblers. But I cannot say that I am convinced of the truth of the theory here suggested, because there is little or no evidence in its favour. In all the conspicuously coloured members of the group, such as the oyster-catcher (*Himantopus ostra-laegus*), stilt (*H. himantopus*) and avocet (*Recurvirostra avosetta*), the sexes are alike, and the same applies to the related gulls. This might perhaps suggest that the original ancestor was dimorphic, the male only being brightly coloured, but with an eclipse plumage, and the female dull. We should then have two lines of evolution, of which each species would have to take one or the other: in the first, the female assumed the arctic characters and the eclipse plumage disappeared; in the second, the arctic characters changed and became toned down. But the whole thing seems decidedly far-fetched. Besides which, a good deal depends on what the enemies of these birds are. If they are hawks and other winged creatures, I am by no means sure that the oyster catcher, at any rate, is not as well off as any. At least I know from personal experience that oyster catchers quietly feeding on the rocks are practically invisible at 100 ft., if one is that distance directly above them. A satisfactory solution of this problem is still to be found.

Summarising the contents of this and the preceding paper⁽¹⁾, we see that they have been concerned rather with stating problems than with affording solutions. These problems call for the combined attack of the

¹ Although not usually called eclipse plumage, the winter plumage of such birds as the waders cannot be logically separated from true eclipse plumage, since all gradations between the two extremes exist.

physiologist, the geneticist and the phylogenist, with help from the field naturalist in unravelling the life histories of the key species. The physiologists' problem is: Why should certain characters be apparently incapable of expression in the female sex? The problem for the geneticist is: What is the genetical basis of this limitation and of the change that enables these characters to be expressed in exceptional cases? The phylogenist's problem is: What is the mechanism at work which prevents the transference of these characters to the female if suitable variations arise?

ACKNOWLEDGMENTS

I have once more to acknowledge my indebtedness to Professor Julian Huxley for helpful advice and illuminating criticism.

REFERENCES.

- (1) WINTERBOTTOM, J. M. (1929). "Studies in sexual phenomena. VII. The transference of male secondary sexual characters to the female." *Journ. Gen.* **xxi**, 367.
- (2) BATES, G. L. (1930). *A Handbook of the Birds of West Africa*.
- (3) FINN, F. (1926). *Wildfowl of the World*.
- (4) BEEBE, C. W. (1906). *The American Naturalist*, **xlii**, 34.
- (5) GOLDSCHMIDT, R. (1923). *The Mechanism and Physiology of Sex Determination*, Engl. trans.
- (6) CREW, F. A. E. (1927). "Studies on the relation of gonadic structure to plumage character in the domestic fowl. III. The laying hen with cock's plumage," *Proc. Roy. Soc. B*, **ci**, 514.
- (7) BEEBE, C. W. (1918). *A Monograph of the Pheasants*.
- (8) WINTERBOTTOM, J. M. (1932). "Field notes from the Gold Coast," *The Ibis*, **xx**.
- (9) HOWARD, H. E. (1920). *Territory in Bird Life*.
- (10) OGLIVIE-GRANT, W. R. (1921). *Guide to the Gallery of Birds*.
- (11) WARD, ROWLAND (1911). *Sportsman's Handbook*.
- (12) BANNERMAN, D. A. (1930). *The Birds of Tropical West Africa*, **i**.
- (13) DARWIN, C. (1871). *The Descent of Man*.
- (14) PYCRAFT, W. P. (1910). *A History of Birds*.
- (15) GOULD, J. (1861). *Monograph of the Trochilidae*.
- (16) ALLEN, G. M. (1930). "Birds of Liberia," *The African Republic of Liberia and the Belgian Congo*, **ii**, 636.
- (17) ALEXANDER, W. B. (1928). *Birds of the Ocean*.
- (18) ROWAN, W. (1926). "On photoperiodism, reproductive periodicity, and the annual migrations of birds and certain fishes." *Proc. Boston Soc. N.H.* **xxxviii**, 147.
- (19) NICHOLSON, E. M. (1927). *How Birds Live*.

- (20) GREENWOOD, A. W. and BLYTH, J. S. (1930). "Some experiments relating to ovarian function in the fowl." *Report of Proceedings of Fourth World's Poultry Congress*, Sect. A, No. 8.
- (21) LILLIE, F. R. (1917). "The Freemartin: A study of the action of sex hormones in the foetal life of cattle." *Journ. Exp. Zool.* xxiii.
- (22) GOODALE, H. D. (1916). "Gonadectomy in relation to the secondary sexual characters of some domestic birds." *Publ.* 243, *Carnegie Inst. Wash.*