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BLOOD PARASITES OF BIRDS IN CENTRAL EUROPE. 3. PLASMODIUM AND HAEMOPROTEUS

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Abstract. The present paper is the third in the series on blood parasites of birds in Central Europe. It is devoted to the genera *Plasmodium* and *Haemoproteus*. *Plasmodium* has been found in 11.3 % of birds belonging to 54 species, most abundant being in Galliformes and Columbiformes. On the other hand, this parasite seems to be absent in Anseriformes, Falconiformes, Hirundinidae and Sturnidae in Central Europe. *Haemoproteus* has been encountered in the studied region in 11.8 % of birds belonging to 85 species. It is most abundant in Falconiformes, Strigiformes, Hirundinidae, Emberizidae, Fringillidae, Muscicapidae, Paridae and Turdidae, but it has not been encountered in Anseriformes. The paper also discusses the dependence of the incidence of these parasites on migratory ability of their hosts and on the nest ecology of birds. Moreover, an ecological outline is given of the representatives of the genera *Plasmodium* and *Haemoproteus* in birds in Central Europe, mainly on the basis of the ecological model of avian malaria after Beaudoin et al. (1971).

In the previous paper of the series dealing with the distribution of avian haematozoa in Central Europe parasites of the genus *Leucocytozoon* were treated (Kučera 1981b). The present paper is devoted to the related two genera of the Haemosporidia, to *Plasmodium* and *Haemoproteus*. It summarizes data on the incidence of these parasites in free-living birds in Central Europe. Their incidence in domestic birds in the region under study was comprehensively treated in the first paper of the series (Kučera 1981a).

MATERIAL AND METHODS

The data on the incidence of the representatives of *Plasmodium* and *Haemoproteus* in Central Europe were gained from papers of various authors mentioned in the first paper of this series (Kučera 1981a) and were treated by methods mentioned in the same paper. In the case of *Plasmodium* data were used from 9 569 and in the case of *Haemoproteus* from 10 094 free-living birds belonging to 173 species in order to carry out numerical evaluation of the incidence of these parasites.

RESULTS AND DISCUSSION

1. Incidence of *Plasmodium* and *Haemoproteus* within different systematic groups of birds

As evident from Table 1 and Fig. 1, the parasites of the genus *Plasmodium* were encountered in 11.3 % of birds belonging to 54 species, and *Haemoproteus* in 11.8 % of birds belonging to 85 species. As in the case of the genus *Leucocytozoon* it should be emphasized, that in many systematic bird groups there are none, or very incomplete data on the incidence of these blood parasites. This applies to Gaviiformes, Podicipedi-

Table 1. Alphabetical list of birds positive for *Plasmodium* and *Haemoproteus* in Central Europe

Plasmodium: *Acrocephalus schoenobaenus* (L.), *Alauda arvensis* L., *Alectoris graeca* (Meisner), *Anthus trivialis* (L.), *Asio flammeus* (Pontoppidan)*, *Asio otus* (L.), *Athene noctua* (Scopoli), *Caprimulgus*

europaeus L., *Carduelis carduelis* (L). *C. chloris* (L.), *C. spinus* (L.), *Circus aeruginosus* (L.)?**, *Coccothraustes coccothraustes* (L.), *Columba palumbus* L., *Corvus corone* L., C. *frugilegus* L., *C. monedula* L., *Emberiza citrinella* L., *Erithacus rubecula* (L.), *Falco tinnunculus* L.?**, ***, *Ficedula hypoleuca* (Pallas), *Fringilla coelebs* L., *Garrulus glandarius* (L.), *Lanius collurio* L., *L. excubitor* L., *Larus canus* L., *Lullula arborea* (L.), *Luscinia megarhynchos* C. L. Brehm, *Lyrurus tetrix* (L.), *Motacilla cinerea* Tunstall, *M. flava* L., *Parus caeruleus* L., *P. major* L., *Passer domesticus* (L.), *P. montanus* (L.), *Perdix perdix* (L.), *Phasianus colchicus* L., *Phoenicurus phoenicurus* (L.), *Phylloscopus collybita* (Vieillot), *Pica pica* (L.), *Prunella modularis* (L.), *Pyrrhula pyrrhula* (L.), *Serinus serinus* (L.), *Sitta europaea* L., *Strix aluco* L., *Sylvia atricapilla* (L.) *S. borin* (Boddaert), *S. communis* Latham, *Troglodytes troglodytes* (L.) *Turdus iliacus* L., *T. merula* L., *T. philomelos* C. L. Brehm, *T. pilaris* L., *Tyto alba* (Scopoli)?****. Total 54 species.

Haemoproteus: *Acanthis canabina* (L.), *A. flammea* (L.), *Accipiter gentilis* (L.), *A. nisus* (L.), *Acrocephalus arundinaceus* (L.), *A. palustris* (Bechstein), *A. schoenobaenus* (L.), *A. scirpaceus* (Hermann), *Alauda arvensis* L., *Anthus trivialis* (L.), *Asio flammeus* (Pontoppidan), *A. otus* (L.), *Athene noctua* (Scopoli), *Botaurus stellaris* (L.), *Buteo buteo* (L.), *Caprimulgus europaeus* L., *Carduelis carduelis* (L.), *C. chloris* (L.), *C. spinus* (L.), *Circus aeruginosus* (L.), *Coccothraustes coccothraustes* (L.), *Columba palumbus* L., *Corvus corone* L., *C. frugilegus* L., *Delichon urbica* (L.), *Emberiza cia* L., *E. citrinella* L., *Erithacus rubecula* (L.), *Falco subbuteo* L., *F. tinnunculus* L., *Ficedula hypoleuca* (Pallas), *Fringilla coelebs* L., *Gallus domesticus*, *Garrulus glandarius* (L.), *Hippolais icterina* (Vieillot), *Hirundo rustica* L., *Lanius collurio* L., *L. excubitor* L., *Loxia curvirostra* L., *Lullula arborea* (L.), *Lyrurus tetrix* (L.), *Motacilla alba* L., *M. flava* L., *Milvus milvus* (L)., *Muscicapa striata* (Pallas), *Oenanthe oenanthe* (L.), *Parus ater* L., *P. caeruleus* L., *P. major* L., *P. montanus* (Baldenstein), *P. palustris* L., *Passer domesticus* (L.), *P. montanus* (L.), *Perdix perdix* (L.), *Phasianus colchicus* L., *Phoenicurus phoenicurus* (L.), *Phylloscopus bonelli* (Vieillot)?****, *P. collybita* (Vieillot), *P. sibilathrix* (Bechstein), *P. trochilus* (L.), *Prunella colaris* (Scopoli), *P. modularis* (L.), *Pyrrhula pyrrhula* (L.), *Riparia riparia* (L.), *Saxicola rubetra* (L.), *Scolopax rusticola* L., *Serinus serinus* (L.), *Sitta europaea* L., *Streptopelia turtur* (L.), *Strix aluco* L., *Sturnus vulgaris* L., *Sylvia atricapilla* (L.), *S. borin* (Boddaert), *S. communis* Latham, *S. curruca* (L.), *S. hortensis* (Gmelin), *Tetrao urogallus* L., *Troglodytes troglodytes* (L.), *Turdus iliacus* L., *T. merula* L., *T. philomelos* C. L. Brehm, *T. pilaris* L., *T. viscivorus* L., *Tyto alba* (Scopoli)*****, *Vanellus vanellus* (L.). Total 85 species.

Note *Galli-Valerio (1931) mentions as "Hemosporidia with schizogony"; **Kučera (1978) reports an indefinable case between *Plasmodium* and *Haemoproteus*; ***Galli-Valerio (1933) states as "gamètes de la malaria"; ****Galli-Valerio (1930) presents as *Halteridium*, but it remains uncertain whether this is the case of *Plasmodium* or *Haemoproteus;* *****Pfeiffer (1890): indefinable case between *Plasmodium* and *Haemoproteus*.

formes, Procellariiformes, Gruiformes, Cuculiformes, Caprimulgiformes, and within the passerines to the family Oriolidae, Remizidae, Cinclidae and Bombycillidae. Likewise the data on the incidence in Pelecaniformes, Ciconiiformes, Apodiformes, Coraciiformes, Piciformes, Alaudidae, Aegithalidae, Certhiidae, Sittidae, Troglodytidae and Laniidae are statistically insignificant because they are based on a material of less than 100 birds examined.

In those groups, from which data are available from at least 100 birds examined, *Plasmodium* is most frequently encountered in Galliformes (38.3 % positive birds) and Columbiformes (20.9 %). Relatively frequently it is also to be found in Strigiformes (2.3 %) and within Passeriformes (3.0 %) in Emberizidae (6.5 %), Fringillidae (5.8 %), Passeridae (4.3 %), Turdidae (3.8 %), Corvidae (3.2 %), Prunellidae (2.9 %), Sylviidae (2.5 %) and Motacillidae (1.9 %). This parasite was more rare in Charadriiformes (1.0 %), Muscicapidae (0.9 %) and Paridae (0.7 %). So far *Plasmodium* has not been found in Anseriformes (291 birds examined), Falconiformes (333 birds examined), Hirundinidae (611 birds examined) and Sturnidae (169 birds examined). Due to the high numbers of negative birds examined in these groups it may be presumed that *Plasmodium* is absent in them. In bird groups with insufficient data on the incidence of *Plasmodium* (see above) the parasites of this genus were also found in Caprimulgiformes, Alaudidae, Sittidae, Troglodytidae and Laniidae.

Haemoproteus was most frequently encountered in Falconiformes (53.1 % of positive birds), Strigiformes (22.6 %) and as regards passerines (12.5 %) in Hirundinidae

(28.5 %), Emberizidae (19.5 %), Fringillidae (15.6 %), Muscicapidae (15.4 %), Paridae (12.7 %) and Turdidae (10.2 %). It was relatively abundant in Sylviidae (9.7 %), Prunellidae (9.6 %), Columbiformes (9.0 %), Galliformes (5.8 %), Passeridae (4.1 %), Motacillidae (3.3 %), Charadriiformes (3.0 %), Sturnidae (3.0 %) and Corvidae (1.6 %). It was also found in Ciconiiformes, Caprimulgiformes, Alaudidae, Sittidae, Troglodytidae and Laniidae, but from these bird groups only incomplete data are available (see above).

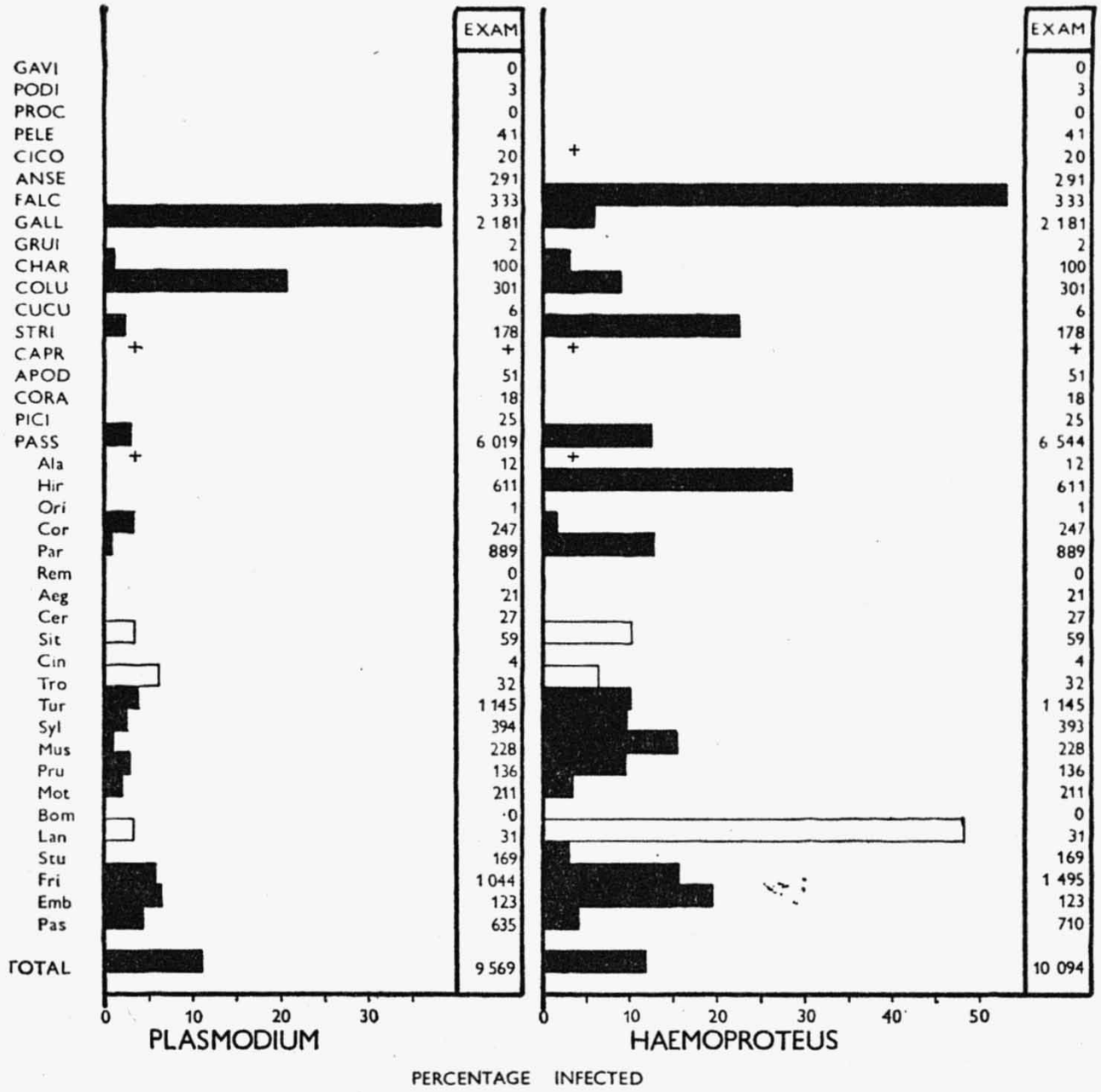

Fig. 1. A graph depicting the incidence of *Plasmodium* and *Haemoproteus* in different systematic groups of birds in Central Europe. (GAVI = Gaviiformes, PODI = Podicipediformes, PROC = Procellariiformes, PELE = Pelecaniformes, CICO = Ciconiiformes, ANSE = Anseriformes, FALC = Falconiformes, GALL = Galliformes, GRUI = Gruiformes, CHAR = Charadriiformes, COLU = Columbiformes, CUCU = Cuculiformes, STRI = Strigiformes, CAPR = Caprimulgiformes, APOD = Apodiformes, CORA = Coraciiformes, PICI = Piciformes, PASS = Passeriformes, Ala = Alaudidae, Hir = Hirundinidae, Ori = Oriolidae, Cor = Corvidae, Par = Paridae, Rem = Remizidae, Aeg = Aegithalidae, Cer = Certhiidae, Sit = Sittidae, Cin = Cinclidae, Tro = Troglodytidae, Tur = Turdidae, Syl = Sylviidae, Mus = Muscicapidae, Pru = Prunellidae, Mot = Motacillidae, Bom = Bombycillidae, Lan = Laniidae, Stu = Sturnidae, Fri = Fringillidae, Emb = Emberizidae, Pas = Passeridae. + = positive finding with no prevalence data given, ▬ = prevalence data from groups in which over 100 birds were examined, ▭ = groups with less than 100 birds examined.

Haemoproteus seems to be absent in Anseriformes, because it was not encountered in any of 291 free-living representatives of this order.

Interesting is the absence of parasites of the genera *Plasmodium* and *Haemoproteus* in Anseriformes living in Central Europe, while in North America, for instance, these protozoa are relatively abundant in this order of birds (Greiner et al. 1975). Likewise *Leucocytozoon* is found in Anseriformes very sporadically, as has been discussed in the previous papers (Kučera 1981a, b). Exact explanation of the absence of blood parasites in Anseriformes in Central Europe is rather impossible on the basis of our present knowledge. It may be only stated that their absence is likely to be caused by unsuitable ecological conditions for the transmission and survival of the given species of parasites in the region studied. The same may be said about the observed absence of parasites of the genus *Plasmodium* in Falconiformes, Hirundinidae and Sturnidae. In these bird groups however, *Haemoproteus* is quite frequent. In this connection it should be said that in diagnosing these parasites by means of blood smears some species of *Plasmodium*, if the infection is mild, may be mistaken for parasites of the genus *Haemoproteus* (Garnham 1966).

If we compare the available data on the incidence of *Plasmodium* and *Haemoproteus* parasites in Central Europe with those in North America (Greiner et al. 1975) and SE Asia (McClure et al. 1978), it may be said that birds of particular systematic groups such as Falconiformes, Strigiformes, Galliformes, Columbiformes, Corvidae, Turdidae, Motacillidae, Sylviidae, Fringillidae and Emberizidae generally show a high predisposition either for *Plasmodium* or for *Haemoproteus*, but most often for parasites of both genera and simultaneously also for *Leucocytozoon* (Kučera 1981b). After a detailed comparison, however, certain and sometimes considerable differences are revealed in the incidence of these parasites in some systematic groups of birds in the areas compared e.g. *Haemoproteus* in North America is practically absent in Sylviidae and it is rarely encountered in Paridae, Hirundinidae, Sturnidae and Passeridae despite the fact that in Central Europe it is abundant in these birds and in some groups its incidence is even very high. If we compare the total incidence in all birds of North America, Central Europe and SE Asia, we see that *Haemoproteus* occurs in all three continents in approximately equal numbers. On the other hand, *Plasmodium* seems to be most abundant in Central Europe and is rather rare in SE Asia.

In South America (Venezuela) Gabaldon et al. (1974, 1975, 1976) found a relatively low incidence of all avian haematozoa, including *Plasmodium* and *Haemoproteus*. The same authors (Gabaldon and Ulloa 1978) later found out that parasites of the genus *Plasmodium* in this region occurred in the peripheral blood of young in the nest (as many as 44 %), while in adult birds mostly chronic and erroneously diagnosed infections were to be considered. In this connection it should be noted that the method of blood smears is very unreliable diagnostic means in the genus *Plasmodium*, but so far, no other more suitable method is available which would make the examination of birds in the field for the presence of these parasites possible. The results obtained by Gabaldon et al. (1974, 1975, 1976, 1978) were confirmed by White et al. (1978). The summarized results of studies on the incidence of blood parasites in the neotropic region, carried out by the last mentioned authors, indicate a low incidence of almost all these parasites in the given region. Only *Haemoproteus* is rather more abundant here than indicated by Gabaldon et al. from Venezuela.

Likewise in the tropical Africa, according to the data summed up after Bennet et al. (1974), Ashford et al. (1976), Bennet and Herman (1976), Wink and Bennet (1976) and Peirce et al. (1977), there is hardly any difference in the total incidence of parasites of the genera *Plasmodium* and *Haemoproteus* from their incidence in Central Europe.

2. Incidence of *Plasmodium* and *Haemoproteus* depending on some ecological properties of their hosts

Fig. 2. graphically shows the incidence of protozoa of the genera *Plasmodium* and *Haemoproteus* depending on the migratory capabilities of their hosts. Similarly as in the genus *Leucocytozoon* (Kučera 1981b), it is evident that no general dependence of *Plasmodium* and *Haemoproteus* on bird migration can be established. In view of these results and in view of the previous discussion it may be assumed that the overwintering of birds in warmer regions does not significantly influence the incidence of all three genera of agents causing avian malaria.

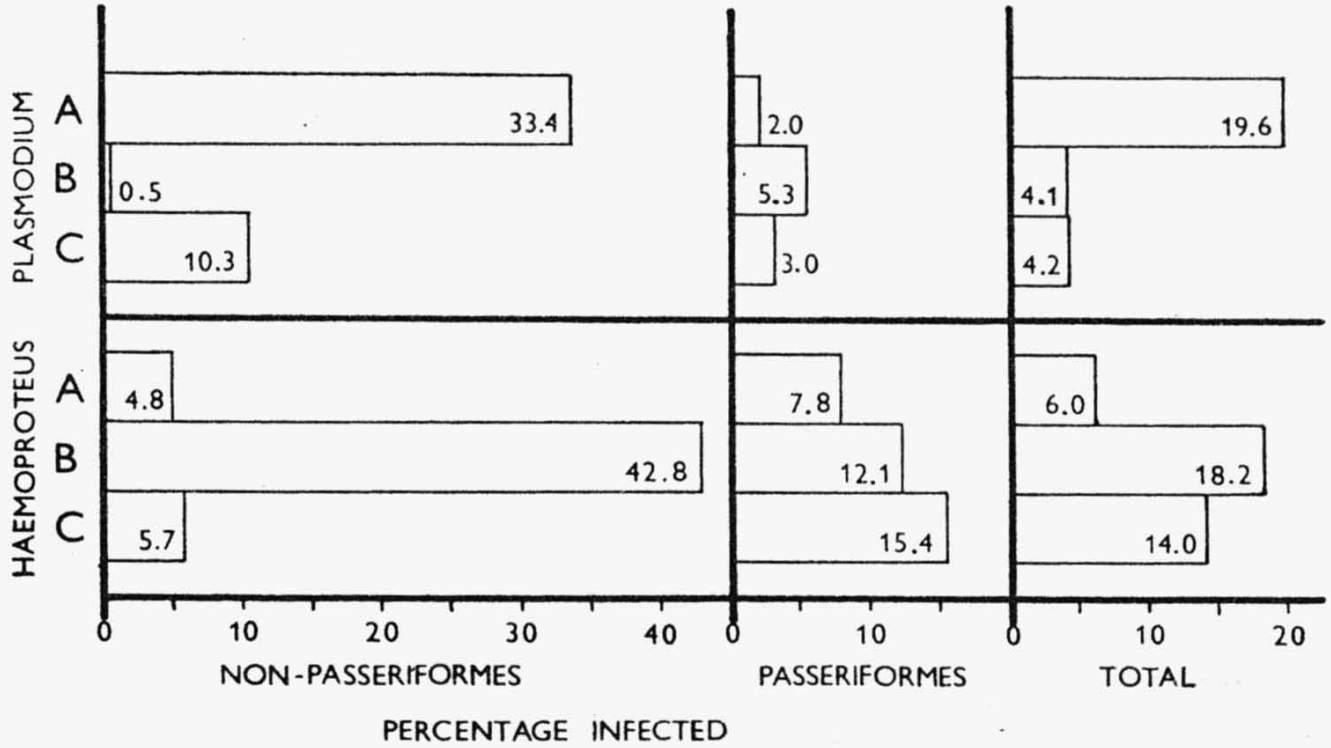

Fig. 2. A comparison between the incidence of *Plasmodium* and *Haemoproteus* in birds of Central Europe categorized according to migration (A = resident birds, B = temporarily migratory birds, C = migratory birds).

In studying the seasonal dynamics of *Plasmodium* and *Haemoproteus* in the peripheral blood of passerines (Fig. 3) on the basis of his own material collected from localities of similar character in Bohemia, the author could trace some differences in both these parasites, even with regard to *Leucocytozoon*. In the spring *Haemoproteus* and *Plasmodium* appear in the peripheral blood of passerines somewhat later than *Leucocytozoon*. While the incidence of *Leucocytozoon* is maintained throughout the season (except its peak in September) on a more or less equal level, the seasonal dynamics of parasites of the genus *Haemoproteus* show two significant peaks. During the spring months the incidence of these parasites gradually increases, reaching its peak in May. i.e. in the period of the growing peak of the nesting activity of birds. As discussed previously (Kučera 1981b) this peak corresponds with relapses of chronic infections in adult birds, evidently caused by their increased sexual activity in this period (Chernin 1952, Rogge 1966, 1968, Haberkorn 1968, Beaudoin et al. 1971 etc.). During the summer and autumn tke incidence of *Haemoproteus* gradually decreases, only reaching another peak in September. As in the genus *Leucocytozoon*, this peak is apparently caused by the fact that in this period the young birds are predominant in the birds' population, in which the infection is mostly in acute stage and therefore easily

detectable by blood smears (Kučera 1981b). Likewise *Plasmodium* was found to be most abundant in the peripheral blood of passerines in May (Fig. 3), while in the remaining months it was encountered quite accidentally. It is possible that this was caused by failure of blood smears as a diagnostic method for plasmodia (see above). In the winter months neither *Haemoproteus* nor *Plasmodium*, similarly as *Leucocytozoon*, were found in the peripheral blood of passerines.

Fig. 4 graphically shows the incidence of the genera *Plasmodium* and *Haemoproteus* in passerines of different age. The graph is based on the same material as Fig. 3. Unlike *Leucocytozoon*, *Plasmodium* and *Haemoproteus* were not encountered in the peripheral

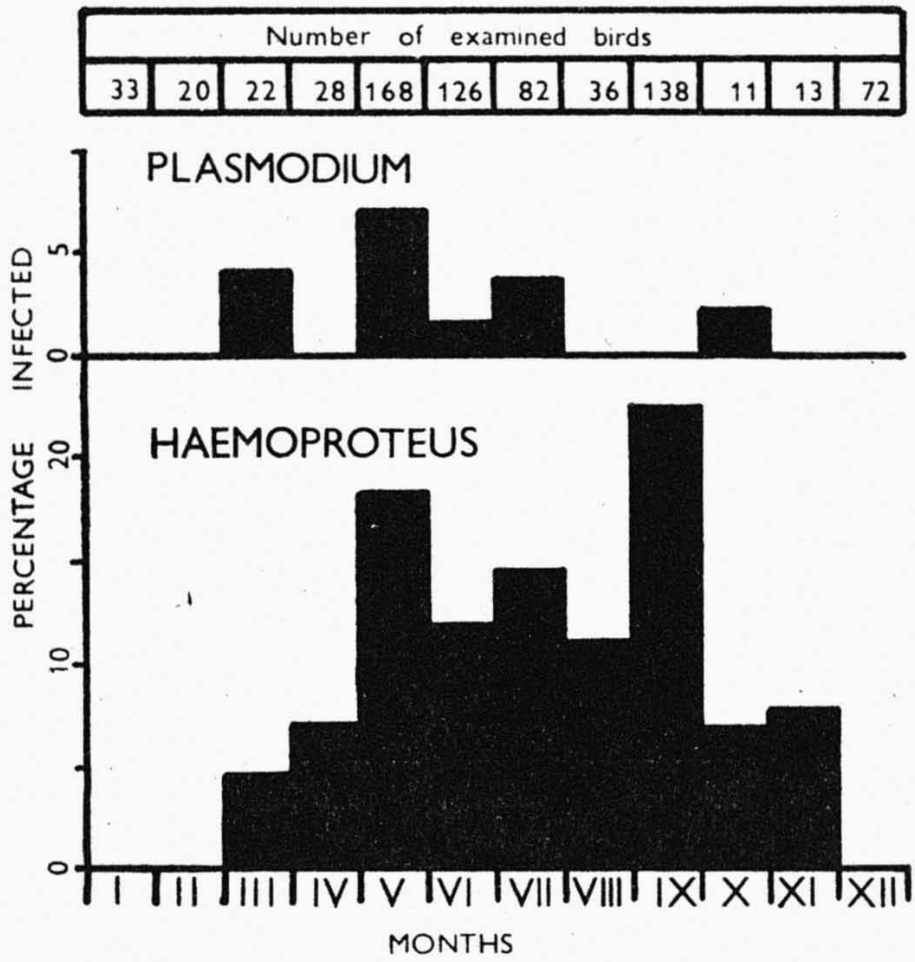

Fig. 3. Incidence of *Plasmodium* and *Haemoproteus* in the peripheral blood of passerines in Bohemia n different months of the year (seasonal dynamics).

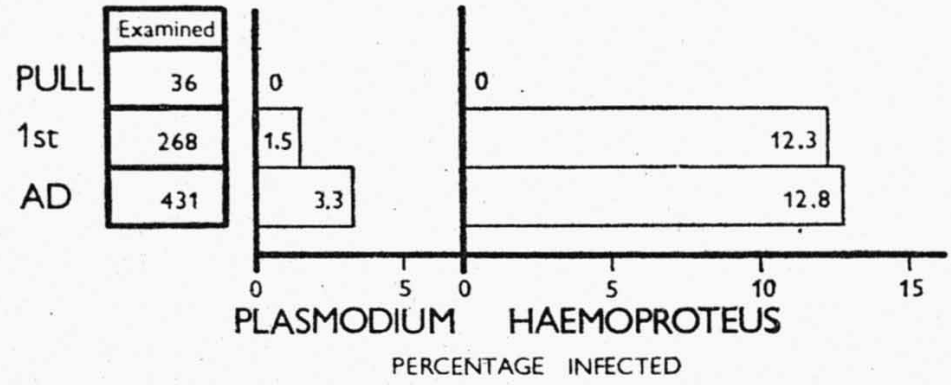

Fig. 4. Incidence of *Plasmodium* and *Haemoproteus* in the peripheral blood of passerines in Bohemia categorized according to age (PULL = nestlings, lst = young birds of the first year, AD = adult birds aged several years).

blood of nestlings, this fact being caused by the nearly equal or longer prepatent period of these parasites (see Garnham 1966 etc.) than the duration of stay of the passerine young in the nest. If the young are infected during their stay in the nest, the blood stages usually appear in them after the young birds have left the nest. Parasites of the genus *Plasmodium* were found by the author of the present paper in about twice as many adult passerines aged several years as in young birds. Similar results were obtained by Geigy et al. (1962) and Lovrics (1967) in Switzerland and by Burtikashvili (1976) in Georgia (USSR). On the other hand, Bennet and Fallis (1960) found some more infected juvenile than adult birds in Canada. No one, however,

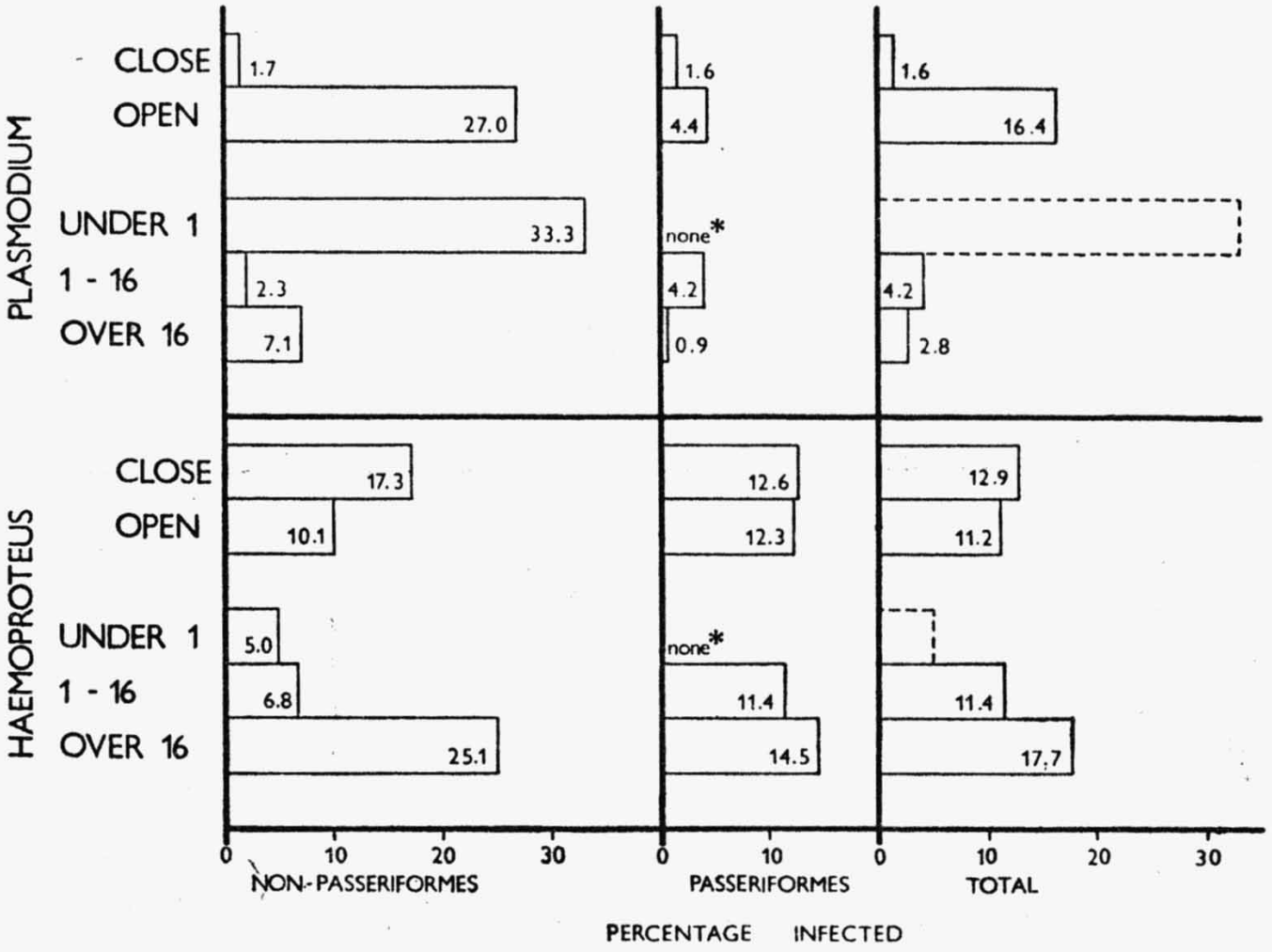

Fig. 5. A comparison between the incidence of *Plasmodium* and *Haemoproteus* in birds of Centra Europe categorized according to the type of nest and according to the duration of stay in the nest (CLOSE = birds with closed type of nest, OPEN = birds with open type of nest, UNDER 1 = birds whose young stay in the nest less than one day after hatching, 1—16 = duration of stay in the nest between one and sixteen days, OVER 16 = duration of stay in the nest over sixteen days, * = no birds examined).

encountered these parasites in nestlings. Gabaldon and Ulloa (1978) reported a high infection rate in nestlings, but in other birds than passerines, and this fact indicates that considerable differences between different orders of birds may be anticipated. The duration of the juvenile period in different bird orders is different after all. Approximately the same percentage of parasites of the genus *Haemoproteus* were found by the author of this paper in young and adult birds. Likewise Bennet and Fallis (1960), Stabler (1961), Geigy et al. (1962), Rogge (1966), Lovrics (1967) and Burtikashvili (1976) reported these parasites mainly in young and adult birds and only exceptionally in nestlings.

Fig. 5. graphically depicts the incidence of parasites of the genera *Plasmodium* and *Haemoproteus* in birds living in Central Europe, categorized according to the type of nest and to the duration of stay of the young in the nest. The graph shows that *Plasmodium* as well as *Leucocytozoon* (Kučera 1981b) occur mostly in those birds which build open nests. In *Haemoproteus*, however, such dependence is not observed. A more or less same percentage of birds of both groups are infected in this case. This phenomenon may be explained by the ecology of insect vectors of the said parasites. Parasites of the genus *Haemoproteus* are transmitted by louse-flies of the family Hippoboscidae (Garnham 1966 etc.) which find refuge not only in the feathers, but also in the

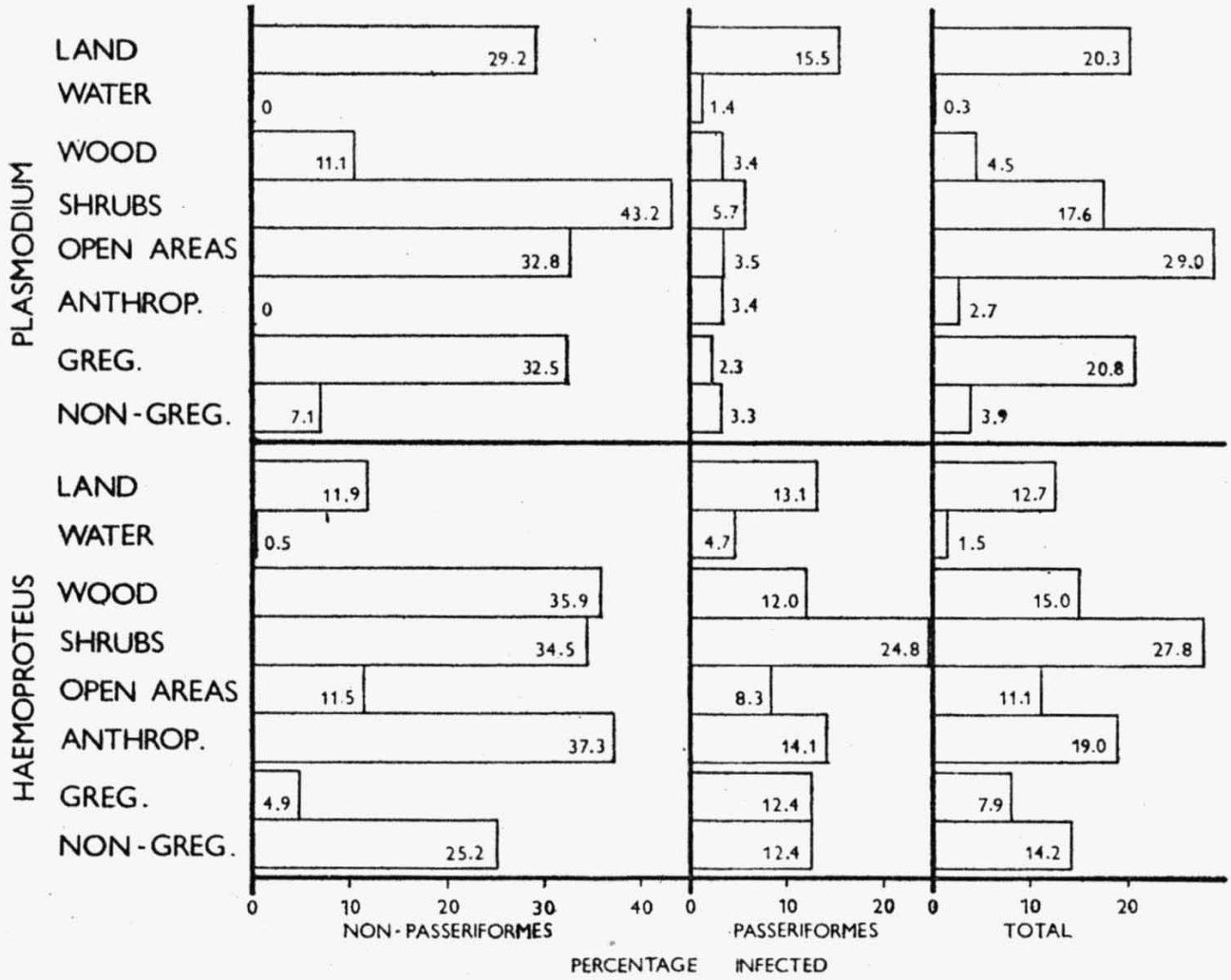

Fig. 6. A comparison between the incidence of *Plasmodium* and *Haemoproteus* in birds of Central Europe categorized according the nest biotope (LAND = terrestrial birds, WOOD = forest birds, WATER = aquatic birds, SHRUBS = shrub birds, OPEN AREAS = birds in fields and other open biotopes, ANTHROP = anthropophilic birds, GREG = gregarious birds, NON-GREG = non-gregarious birds).

nests of birds (Macháček 1977) and do not care whether the nests are open or closed. Therefore the incidence of parasites of this genus does not differ in birds building both types of nests. Other blood parasites are transmitted by insects which fly freely and seek birds only with the purpose of feeding on them. These insects, consequently, find an easy access to the young in open nests and the incidence of blood parasites in them is therefore much higher than in birds with closed nests.

So far as the incidence of the parasites discussed depends on the duration of stay of the young in the nests, (Fig. 5), the genus *Haemoproteus* shows a very distinct

dependence. The longer the stay in the nest, the greater is the predisposition of birds to the blood parasites of this genus. This phenomenon as well as little difference in the rate of infection of the young and older birds with these parasites (see above and Fig. 4) suggest that the major number of infected birds has been infected early in their life, while still in the nest. The longer the stay in the nest, the greater the probability of infection. In parasites of the genus *Plasmodium* such a dependence cannot be traced. Likewise the fact that the infection rate in birds aged several years is higher than in young birds (Fig. 4.) suggests that the transmission of plasmodia to uninfected birds also takes place among old birds.

Fig. 6 depicts a comparison between the evidence of parasites of the genera *Plasmodium* and *Haemoproteus* in bird groups categorized according to the nest biotope. Similarly as in *Leucocytozoon* (Kučera 1981b) it is interesting to note that the infection rate in aquatic birds and in case of *Plasmodium* also in anthropophilic birds, is very low. Likewise, the differences in the incidence of parasites of the genera *Plasmodium* and *Haemoproteus* in non-Passeriformes and Passeriformes categorized in groups of birds inhabiting forest, shrubs and forest-free regions suggest considerable differences in this respect in different bird orders. Moreover, the differences revealed in the incidence of these parasites in gregarious and non-gregarious birds are rather disputable.

In conclusion of the previous paper dealing with parasites of the genus *Leucocytozoon* (Kučera 1981b) the data obtained on the incidence and ecology of these parasites in birds of Central Europe have been discussed, indicating that the ecological model of avian malaria originally concepted by Beaudoin et al. (1971) for the parasites of the genus *Plasmodium* in birds of North America, may be applied. Practically identical discussion may be conducted in the case of parasites of the genera *Plasmodium* and *Haemoproteus*, in which the said ecological model may be applied to the ecology of these parasites in birds of Central Europe.

КРОВЕПАРАЗИТЫ ПТИЦ СРЕДНЕЙ ЕВРОПЫ. 3. *PLASMODIUM* И *HAEMOPROTEUS*

Я. Кучера

Резюме. Работа является третей частью цикла о кровепаразитах птиц в Средней Европе и посвящена проблематике родов *Plasmodium* и *Haemoproteus*. Род *Plasmodium* обнаружен в Средней Европе у 11,3 % птиц, относящихся к 54 видам, чаще всего встречается у Galliformes и Columbiformes. Однако этот паразит очевидно отсутствует у Anseriformes, Falconiformes, Hirundinidae и Sturnidae. Род *Haemoproteus* обнаружен у 11,8 % птиц Средней Европы, относящихся к 85 видам. Он чаще всего встречается у Falconiformes, Strigiformes, Hirundinidae, Emberizidae, Fringillidae. Muscicapidae, Paridae и Turdidae. В изучаемой области его не находили у Anseriformes. В работе также обсуждается зависимость наличия паразитов обоих родов от миграционных способностей их хозяев и от экологии гнездования птиц. В общих чертах также намечена экология представителей родов *Plasmodium* и *Haemoproteus*, встречающихся у птиц Средней Европы, особенно на основании экологической модели птичьей малярии, согласно Бодуэну и др. (Beaudoin et al. 1971).

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